ISSN 0067-1975

RECORDS OF THE AUSTRALIAN MUSEUM

Pacific Tanaidacea (Crustacea): revision of the genus *Agathotanais* with description of three new species .... KIM LARSEN 99

A new genus and two new species of myrophine worm-eels, with comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae) ...... P.H.J. CASTLE & JOHN E. MCCOSKER 113

A new species of the Devonian lungfish *Dipnorhynchus* from Wee Jasper, New South Wales .... K.S.W. CAMPBELL & R.E. BARWICK 123

Monophyly, interrelationships and description of three new genera in the dottyback fish subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae) .... ANTHONY C. GILL & ALASDAIR J. EDWARDS 141

A new species of *Graphium* Scopoli (Lepidoptera: Papilionidae) from the Bismarck Archipelago, Papua New Guinea .... C.J. MÜLLER & W.J. TENNENT 161

A new species of *Cethosia* and a new subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea .... C.J. MÜLLER 169

An unusual micromorphic brachiopod from the Middle Cambrian of north-eastern New South Wales, Australia .... GLENN A BROCK 179

Systematics, biostratigraphy and evolution of the late Ludlow and Přídolí (Late Silurian) graptolites of the Yass district, New South Wales, Australia .. R.B. RICKARDS & A.J. WRIGHT 187

CONTENTS VOLUME 51 (1999) 215

VOLUME 51 NUMBERS 2 & 3 20 OCTOBER 1999

RECORDS OF THE AUSTRALIAN MUSEUM

Editorial Committee:

Chair: J.M. Leis (VERTEBRATE ZOOLOGY)

V.J. Attenbrow (ANTHROPOLOGY)
D.J. Bickel (INVERTEBRATE ZOOLOGY)
G.D. Edgecombe (PALAEONTOLOGY)
A.E. Greer (VERTEBRATE ZOOLOGY)
F.L. Sutherland (GEOLOGY)
G.D.F. Wilson (INVERTEBRATE ZOOLOGY)

Editor: S.F. McEvey
editor@amsg.austmus.gov.au

Director: M. Archer

© Copyright Australian Museum, 1999

No part of this publication may be reproduced without permission of the Editor.

Price AU$33.00
add 10% for postage and handling within Australia
add 20% for postage and handling to other countries

Printed by RodenPrint Pty Ltd, Sydney

ISSN 0067-1975

The Australian Museum's mission is to increase understanding of, and influence public debate on, the natural environment, human societies and human interaction with the environment. The Museum has maintained the highest standards of scholarship in these fields for more than 100 years, and is one of Australia's foremost publishers of original research in anthropology, geology and zoology.

The *Records of the Australian Museum* (ISSN 0067-1975) publishes the results of research that has used Australian Museum collections and studies that relate in other ways to the Museum's mission. There is an emphasis on research in the Australasian, southwest Pacific or Indian Ocean regions. The *Records* is released annually as three issues of one volume, volume 50 was published in 1998. Monographs are published about once a year as *Records of the Australian Museum, Supplements*. Supplement 24 (ISBN 0-7313-8807-0) was published in June 1998. Catalogues, lists and databases have been published since 1988 as numbered *Technical Reports of the Australian Museum* (ISSN 1031-8062). *Technical Report* number 14 was published in March 1999. *Australian Museum Memoirs* (ISSN 0067-1967) ceased in 1983.

These three publications—*Records*, *Supplements* and *Technical Reports*—are distributed to libraries at more than 700 academic institutions throughout the world. Librarians are invited to propose exchange agreements with the Australian Museum Research Library (http://www.austmus.gov.au/is/lib.htm). Back issues are available for purchase direct from the *Australian Museum Scientific Publications* office. Subscriptions are accepted only for the *Records*.

Authors are invited to submit manuscripts presenting results of their original research. Manuscripts meeting subject and stylistic requirements outlined in the *Instructions to Authors* (http://www.austmus.gov.au/info/pub.htm) are assessed by external referees.

www.austmus.gov.au

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 99–112. ISSN 0067-1975

Pacific Tanaidacea (Crustacea): Revision of the Genus *Agathotanais* with Description of Three New Species

KIM LARSEN

Department of Biological Science, Macquarie University, Sydney NSW 2109, Australia
klarsen@rna.bio.mq.edu.au

Present address: Zoological Museum, University of Copenhagen,
Universitetsparken 15, 2100 KBH East, Denmark

ABSTRACT. New Pacific material of the cosmopolitan genus *Agathotanais* Hansen, 1913 has made a generic revision possible. Newly discovered character states for the antenna have made it necessary to modify the generic diagnosis. Three new species—*A. manganicus* and *A. ahyongi* from the central Pacific and *A. spinipoda* from the continental shelf and slope off southeastern Australia–are described, they increase the number of species in the genus to eight. A key to the females of *Agathotanais* species is provided. Sexual dimorphism is generally restricted to the presence of pleopods in the male. The characters defining *Agathotanais* are considered apomorphic within the Tanaidomorpha. The distribution pattern of *Agathotanais* is discussed.

LARSEN, KIM, 1999. Pacific Tanaidacea (Crustacea): revision of the genus *Agathotanais* with description of three new species. *Records of the Australian Museum* 51(2): 99–112.

The vast abyssal plain of the Pacific Ocean is practically unexplored. Within the Pacific, the Australian region represents an area of particular interest since Australia was the last landmass to separate from Antarctica. The Australian crustacean fauna is considered both archaic and diverse (Poore & Wilson, 1993). The southern region of Australia contains elements derived from the Tertiary circumpolar Weddellian fauna (Poore, 1994). Because of the long period of isolation, Australia has a high degree of endemicity (e.g., about 90% for isopod crustaceans, N.L. Bruce, pers. comm.). This region has, therefore, the greatest potential for discovery of new invertebrates (Poore *et al.*, 1994).

Hansen erected the genus *Agathotanais* in 1913 for the species *Agathotanais ingolfi*. The latter is found in large numbers throughout the deep North Atlantic (Hansen, 1913; Lang, 1971b; Bird & Holdich, 1988; Larsen, in press). Subsequently, four closely related species have been described. *Agathotanais splendius* Kudinova-Pasternak, 1970 from the northwest Pacific (2 specimens), *A. hanseni* Lang, 1971b from the Central American Pacific slope (5 specimens), *A. ghilarovi* Kudinova-Pasternak, 1989 from the Indian Ocean (29 specimens) and *A. brevis* Kudinova-Pasternak, 1990 from the South Atlantic (1 specimen). The genus is represented in all oceanic regions of the world.

Materials and methods

Types and other specimens of *Agathotanais manganicus* n.sp. and *A. ahyongi* n.sp. are deposited at the Australian Museum (AM). Types and other specimens of *A. spinipoda* n.sp. are in the Museum of Victoria (MV), Melbourne. Paratypes of *A. hanseni* are deposited in the American Museum of Natural History (AMNH), New York. Paratypes of *A. ingolfi* are located in the Zoological Museum of the University of Copenhagen (ZMUC), Denmark. Types of *A. splendius, A. brevis* and *A. ghilarovi* are located in the Moscow State University Museum (MSU), Russia.

Station data are given in Table 1. DOMES (Deep Ocean Mining Environmental Study) data were collected by G.D.F. Wilson & party on *RV Oceanographer*—sampler: Sandia 0.25 m^2 box core. Station list data for other "DOMES site A" stations are given in Thistle & Wilson (1987). Slope data were collected by G.C.B. Poore & party and M.F. Gomon & party on *RV Franklin*—sampler: epibenthic sled; station list and data for other "slope" stations are given in Kornicker & Poore (1996).

Table 1. Station list: DOMES (Deep Ocean Mining Environmental Study) site A; Clipperton and Clarion fracture zone; equatorial Pacific abyssal plain. Slope stations: southeastern Australian shelf.

DOMES #1	station DJ02	09°23.52'N	151°32.94'W	5155 m	23 Nov 1977
DOMES #1	station DJ15	09°20.30'N	151°24.10'W	5166 m	26 Nov 1977
DOMES #1	station DJ20	09°19.80'N	151°35.10'W	5260 m	27 Nov 1977
DOMES #1	station DJ23	09°33.23'N	151°38.33'W	4934 m	28 Nov 1977
DOMES #1	station DJ38	09°36.30'N	151°58.00'W	5086 m	03 Dec 1977
DOMES #2	station DJ41	09°22.70'N	151°28.00'W	5191 m	18 May 1978
DOMES #2	station DJ50	09°22.10'N	151°58.00'W	5086 m	20 May 1978
DOMES #2	station DJ66	09°27.00'N	151°35.90'W	5250 m	25 May 1978
DOMES #2	station DJ69	09°15.80'N	151°30.70'W	5049 m	25 May 1978
DOMES #2	station DJ72	09°33.80'N	151°21.30'W	5240 m	27 May 1978
DOMES #2	station DJ73	09°28.10'N	151°15.60'W	5107 m	27 May 1978
DOMES #2	station DJ77	09°21.30'N	151°21.50'W	5034 m	28 May 1978
slope	station 27	38°25.00'S	149°00.00'E	1500 m	22 Jul 1986
slope	station 32	38°21.90'S	149°20.00'E	1000 m	23 Jul 1986
slope	station 33	38°19.60'S	149°24.30'E	930 m	23 Jul 1986
slope	station 40	38°17.70'S	149°11.30'E	400 m	24 Jul 1986
slope	station 53	34°52.72'S	151°15.04'E	996 m	22 Oct 1988
slope	station 67	38°23.95'S	149°17.02'E	1277 m	25 Oct 1988
slope	station 69	38°29.33'S	149°19.98'E	1840 m	26 Oct 1988

Systematics

Suborder Tanaidomorpha Sieg, 1980
Superfamily Paratanoidea Lang, 1949
Family Anarthruridae Lang, 1971a
Subfamily Anarthrurinae Lang, 1971a
Tribe Agathotanaini Lang, 1971a

Genus *Agathotanais* Hansen, 1913

Synonymy. *Agathotanais* Hansen, 1913, 3(3): 8, 63, 64.–Nierstrasz, 1913, 32a: 38.–Barnard, 1920, 17: 331.–Zimmer, 1926, 3(1): 686, 690, 696.–Lang, 1949, 42(18): 7.–Shiino, 1952, 2(2): 63.–Beklemischew, 1958, 1: 268, 298.–Lang, 1968, 1: 160.–Kudinova-Pasternak, 1970, 86: 370.–Lang, 1971a, 21: 57–59.–Lang, 1971b, 23: 363–365.–Sieg, 1973, 33: 282.–Gardiner, 1975, 170: 179.–Sieg, 1976, 14: 178.–Bird & Holdich, 1988, 22: 1592, 1597.–Bird & Holdich, 1989, 23: 137.–Kudinova-Pasternak, 1990, 126: 100.

Diagnosis (modified after Hansen, 1913; Lang, 1971b and Bird & Holdich, 1988): cuticle heavily calcified and deeply pitted. Antennule with 3 articles. Pleon narrower than pereon and pleotelson. Antenna greatly reduced, more so in female than male. Mandible molar process consisting of membranous lobe only. Left mandible lacina mobilis absent or reduced to knoblike process fused with incisor. Maxillule endite with 7–11 spines. Labium with anterolateral processes and mostly with medial plumose setae. Maxilliped endites circular or hexagonal. Except for the distal part of cheliped and pereopod dactylus, all appendages setulose. Chelipeds slender, attached to cephalothorax ventrally and not via carapal sclerite. Pereopods 4–6 dactylus and terminal spine not fused. Uropods short, stout, uniramous and uniarticulate.

Type species: *Agathotanais ingolfi* Hansen, 1913

Gender: masculine.

Remarks. *Agathotanais* is unique within the Tanaidomorpha because of the reduced antenna. Within the Anarthruridae, no other genera display even remotely similar reductions although both the *Paranarthrura* and *Paragathotanais* share some generic features.

Agathotanais splendius and *A. brevis* are incompletely described from few specimens. Specimens of these species could not be obtained for revision. The validity of these species is therefore uncertain.

The status of *A. hanseni* is similarly problematic. Lang (1971b) did not illustrate the diagnostic characters in his description of this species. The holotype is apparently lost (as well as that of *A. ingolfi*) and the paratypes are all in poor condition. One specimen of *A. hanseni* was reported from the Atlantic near the Azores (Lang, 1971b). This specimen, however, could not be located and, considering the identification problems associated with tanaids, the Atlantic record may be a misidentification. Lang (1971b) stated that *A. ingolfi* could be distinguished from *A. hanseni* by the following characters: (*a*) width/length ratio of pereonite 4–5, greater in *A. ingolfi* (P4 = 1.0, P5 = 1.1) than *A. hanseni* (P4 = 0.78, P5 = 0.85); (*b*) anterolateral carapace margins convex for *A. hanseni* and concave for *A. ingolfi*; (*c*) eleven heavy setae on the maxillule of *A. hanseni*, while 10 in *A. ingolfi*. Some specimens in the Northwest Atlantic, however, had convex anterolateral margins (*A. hanseni* character) and a width/length ratio of P4 = 1.0, P5 = 1.05 corresponding to that of *A. ingolfi* (Larsen, in press). The *A. hanseni* paratypes specimens have suffered various degrees of air-drying. They appear to have shrunk in width rather than length thus obscuring this character. Little confirmation is gained from examining the shape of the carapace on the paratypes, because two specimens lack the head altogether and another is male (the males of the two species shows no morphological differences). On the two complete female specimens, the anterior corners of the carapace are convex. The stout setae on the maxillule are not a reliable taxonomic character because they are known to be ontogenetically dependent (Larsen & Wilson, 1998) and are also inconspicuous in the two species (Bird & Holdich, 1988: 1598). The latter authors also suggest caution regarding this character.

Kudinova-Pasternak (1989) illustrates the pleopod as belonging to the female and the mandibles as belonging to the male for *A. ghilarovi*. This, however, is an editorial mistake and the text describe these, correctly, as male pleopods and female mandibles.

Agathotanais manganicus n.sp.

Material examined. HOLOTYPE (AM): 1 ovigerous ♀, DOMES site A, station DJ 23, (body length = 2.9 mm), AM P51003. PARATYPES (AM): 1 nonovigerous ♀, DOMES site A station DJ20, mouthparts and limbs dissected, AM P50999; 1 nonovigerous ♀, DOMES site A station DJ02, cut in two, mounted on SEM stub and coated, AM P50997.

Other material. 1 fragmented ♀, 2 mancas, DOMES site A station DJ23; 1 nonovigerous ♀ (fragmented), DOMES site A station DJ50; 1 ovigerous ♀, DOMES site A station DJ66; 1 juvenile ♀, DOMES site A station DJ72.

Diagnosis of female. Antennule article 1 longer than all distal articles together, antenna with 2 articles, longer than 0.5 length of antennule first article. Pereonite 6 longer than broad.

Etymology. Name refers to the Manganese Nodule Province where the specimens were collected.

Description of adult female (Fig. 1A,B). *Body* cylindrical, slender. *Cephalothorax* (Fig. 1C) shorter than first 2 pereonites combined, anterolateral corners slightly concave. *Pereonites* tapering posteriorly, pereopod shoulders placed anteriorly on pereonites 1–3, about midlength on pereonite 4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long (l/w ratio 0.8), shorter than all other pereonites. *Pereonite 2–6* l/w ratios 1.0, 1.15, 1.5, 1.5, 1.1 respectively. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* as long as last 3 pleonites together, apex margin straight. *Antennule* (Fig. 1M) with 3 articles. *Article 1* longer than rest of antennule, with 1 simple seta midlength and 1 distally. *Article 2* less than 0.25 times article 1 length, with 1 simple seta distally. *Article 3* 0.4 times longer than article 2, cone shaped with 5 simple setae and 1 aesthetasc distally. *Antenna* (Fig. 1N) 2-articulate, longer than 0.5 length of antennule first article, with 2 distal simple setae. *Mouthparts*. *Labrum* (Fig. 1D), distal margin rather flat, setose. *Mandibles*, molar process consisting of only a membranous lobe. *Left mandible* (Fig. 1E) lower part of incisor pointed; lacina mobilis absent. *Right mandible* (Fig. 1F), incisor bifurcate, upper part pointed, lower part blunt. *Maxillule* (Fig. 1H) endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 1I) elongated without recognisable features. *Labium* (Fig. 1J) with anterolateral processes and a plumose spiniform seta midlength. *Maxilliped* (Fig. 1K) basis fused medially. Endite hexagonal, not fused medially and more heavily setose on anterolateral corners. Palp article 1 outer margin longer than inner, smooth; article 2 inner margin longer than outer and with 3 distal setulate setae; article 3 with 3 setulate setae on inner margin; article 4 with 5 distal setulate setae. *Epignath* (Fig. 1L) with distal setules. *Cheliped* (Fig. 2G). *Basis* quadrate, half the length of carpus. *Merus* with 1 simple setae sternally. *Carpus*, about as long as propodus, with 2 simple setae at midlength on sternal margin. *Propodus* (Fig. 2H) with 1 simple seta medially on sternal margin and 1 by dactylus insertion. *Fixed finger* with 3 distal setae on inner margin; distal tooth bifurcate. *Dactylus* with small process by insertion of distal tooth. *Oostegites* (Fig. 1G) originating from pereonite 1–4. Anterior margin of oostegite 1 with scattered setules. *Pereopod 1* (Fig. 2A). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* with 1 distal simple seta on each margin. *Merus* expanding in width distal, half as long as carpus, with 1 distal simple seta on tergal margin. *Carpus* as long as dactylus and terminal spine together, with 1 simple seta on tergal margin and 1 medial on distal margin. *Propodus* 0.25 times longer than carpus, with 1 simple long seta and 2 distal short setae. *Dactylus* and terminal spine shorter than propodus. *Pereopod 2* (Fig. 2B) similar to pereopod 1 except *basis* with 1 seta near midlength on sternal margin; *ischium* smooth; *carpus* with

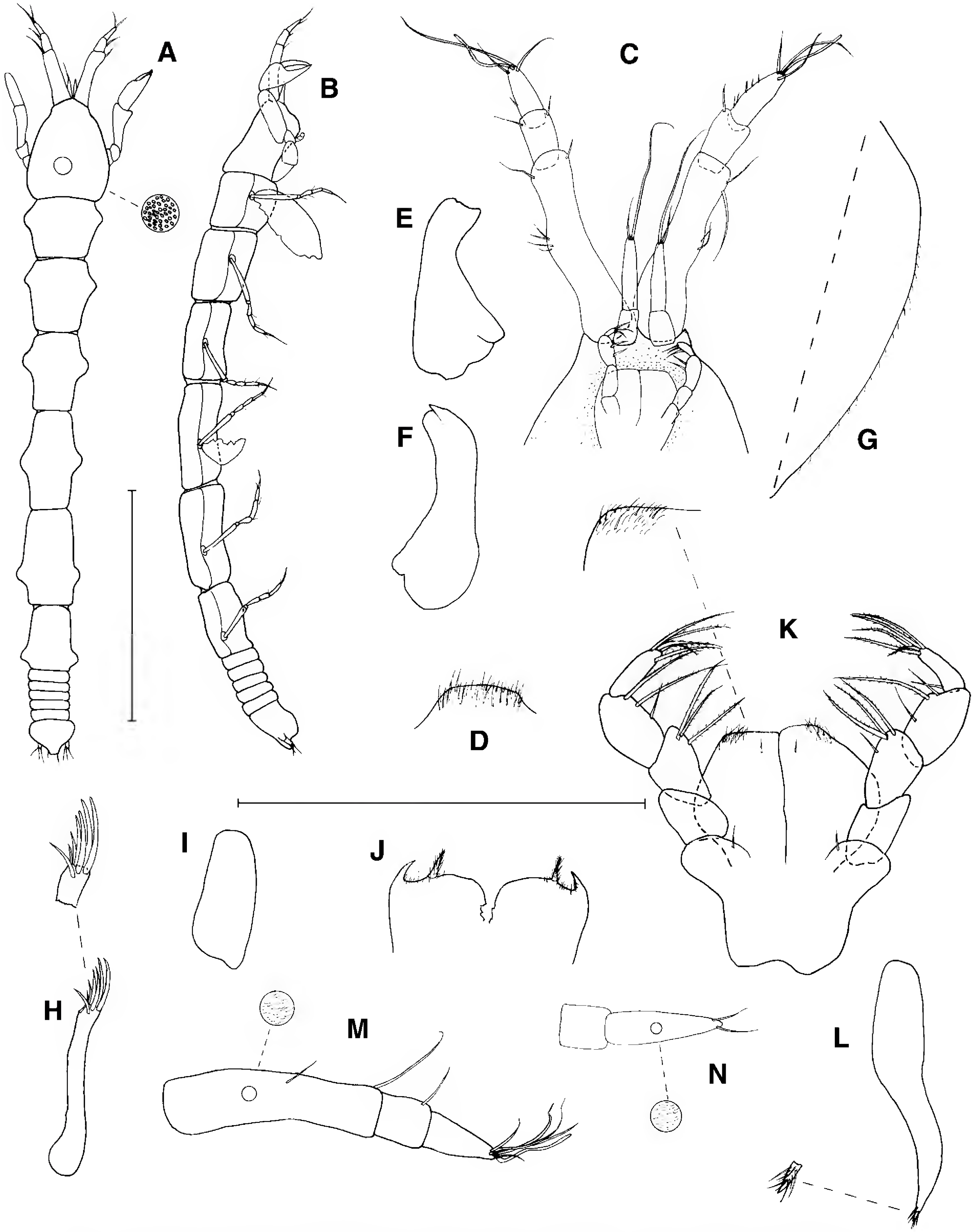


Figure 1. *Agathotanais manganicus* n.sp., A–C, ♀ holotype, AM P51003—A, dorsal view; B, lateral view; C, ventral view of anterior carapace; scale bar for A and B = 1 mm. *Agathotanais manganicus* n.sp. D–N, ♀ paratype, AM P50999—D, labrum; E, left mandible; F, right mandible; G, anterior margin of first oostegite; H, maxillule, palp not shown; I, maxilla; J, labium; K, maxilliped; L, epignath; M, antennule; N, antenna; scale bar for mouthparts = 0.25 mm.

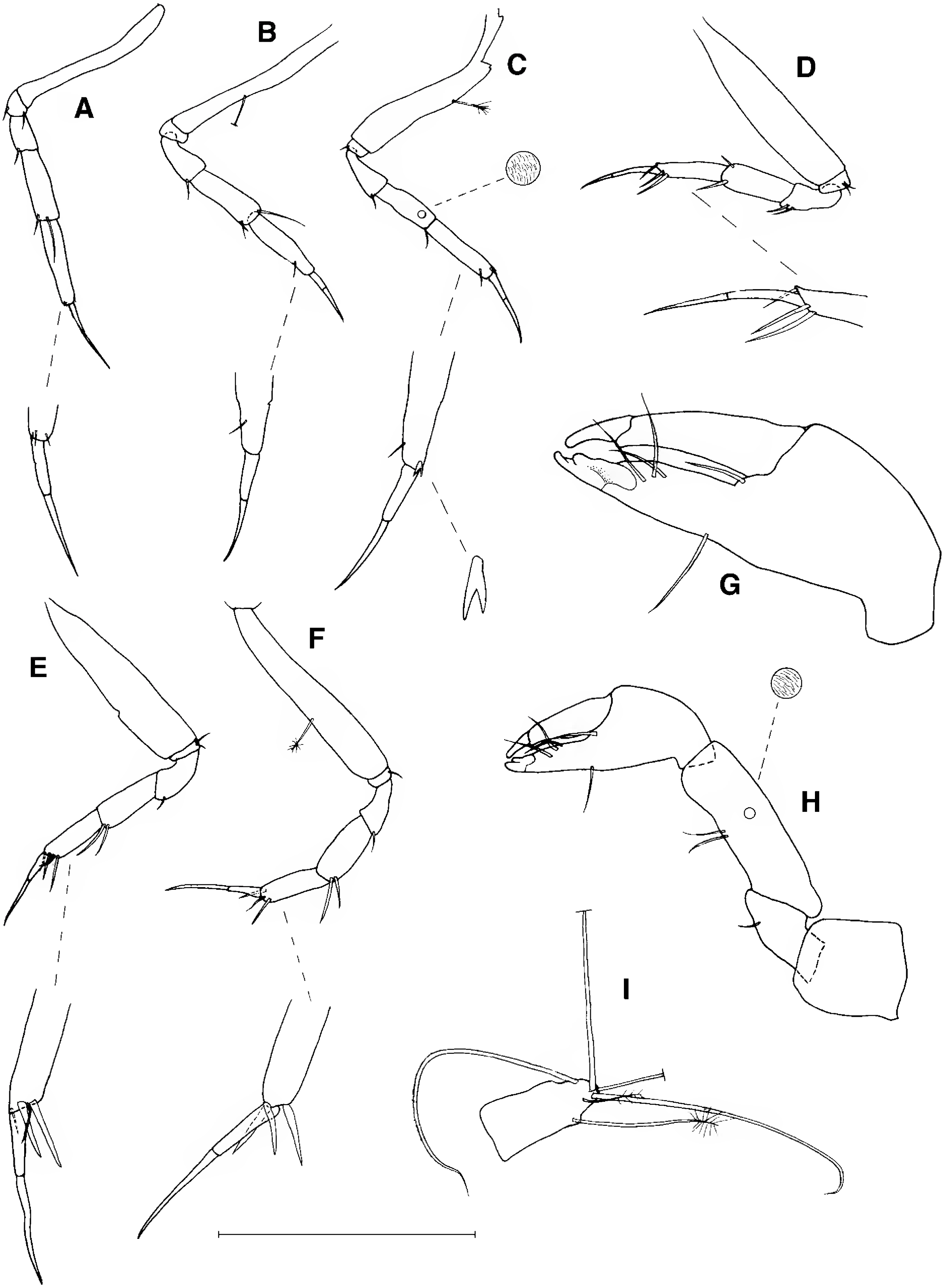


Figure 2. *Agathotanais manganicus* n.sp., ♀ paratype AM P50999—A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, cheliped; H, cheliped propodus and dactylus; I, uropod; scale bar = 0.3 mm.

2 distal simple setae on tergal margin and 1 sternally; *propodus* with 1 short simple seta on tergal margin. *Pereopod 3* (Fig. 2C) similar to pereopod 1 except *basis* with 1 plumose seta near midlength on sternal margin; *ischium* with 1 seta only; *carpus* with 1 distal seta on tergal margin; *propodus* with 1 short simple seta on tergal margin, and a denticulate scale on sternal margin. *Pereopod 4* (Fig. 2D) similar to pereopod 1 except *basis* somewhat wider; *merus* with 2 distal simple stout setae on tergal margin; *carpus* with 1 distal simple stout seta on tergal margin and 1 simple short seta on sternal margin; *propodus* with 2 distal simple stout setae on tergal margin and 1 simple short seta on sternal margin. *Pereopod 5* (Fig. 2E) similar to pereopod 4 except *merus* with 1 distal simple seta on tergal margin; *carpus* with 2 distal simple stout setae on tergal margin. *Pereopod 6* (Fig. 2F) similar to pereopod 4 except *basis* with 1 plumose seta midlength on sternal margin; *ischium* with 1 simple seta only; *merus* with 1 distal simple seta on tergal margin; *carpus* with 2 distal simple stout setae on tergal margin; *propodus* with 3 distal simple stout setae on tergal margin. *Pleopods* absent in females. *Uropods* (Fig. 2I) uniramous. *Endopod* uniarticulate, with 3 long, 1 short simple and 1 short plumose seta distally, exopodal process with 1 long distal plumose long.

Remarks. The unique two articulated antenna of *Agathotanais manganicus* n.sp. is considered the most pleisiomorphic condition within *Agathotanais* and made it necessary to modify the generic diagnosis.

Agathotanais ahyongi n.sp.

Material examined. HOLOTYPE (AM): 1 nonovigerous ♀ (body length 3.7 mm), DOMES site A station DJ69, AM P51007. PARATYPES: 1 nonovigerous ♀, mouthparts and limbs dissected; 1 ♂, 1 juvenile ♀, 2 mancas, DOMES site A station DJ73, AM P51009. 1 nonovigerous ♀, DOMES site A station DJ38, cut in two, mounted on SEM stub and coated, AM P51002. 1 ♂, DOMES site A station DJ 77, AM P51013.

Diagnosis. Antennule article 1 no longer than rest of antennule. Antenna reduced into lobes not visible in the compound scope. *Labium* without median plumose seta. Pereonite 6 longer than broad (l/w ratio 1.4).

Etymology. Named after my friend and fellow student Shane T. Ahyong.

Description of adult female (Fig. 3A,B). *Body* cylindrical, slender. *Cephalothorax* (Fig. 3O) shorter than first 2 pereonites; anterolateral corners convex. *Pereonites*. Pereopod shoulders placed anteriorly on pereonite 1, near midlength on pereonites 2–4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long l/w ratio 0.9, shorter than other pereonites. *Pereonite 2–6* l/w ratio 1.3, 1.4, 1.6, 1.7, 1.4 respectively. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* longer than last 3 pleonites together, rounded in lateral view, apex margin straight. *Antennule* (Fig. 3E) with 3 articles. *Article 1* as long as rest of antennule, with 1 simple seta midlength and 3 distally. *Article 2* less than 0.5 times of article 3 length, smooth. *Article 3* with 4 long setae distally. *Antenna* (Fig. 3N). Minute lobe-like structures without setae. *Mouthparts*. *Labrum* (Fig. 3G), distal margin with small medial lobe, setose. *Labium* (Fig. 3L) with anterolateral processes but without plumose seta midlength. *Mandibles* molar process consists of membranous lobe only. *Left mandible* (Fig. 3H) 0.3 times larger than right mandible; incisor with 3 denticles; lacina consisting of 1 small lobe and a minute accessory lobe. *Right mandible* (Fig. 3I) incisor with 3 denticles. *Maxillule* (Fig. 3J) endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 3K) elongate without recognisable features. *Maxilliped* (Fig. 3M) basis fused medially. Endite elongate, not fused medially and more heavily setose on anterolateral corners. Palp article 1 quadrate, smooth; article 2 rectangular, with 1 distal seta; article 3 with 2 setae on inner margin; article 4 with 4 distal setae. *Epignath* not found. *Cheliped* (Fig. 4A). *Basis* rectangular, less than half length of carpus. *Merus* smooth, ovoid. *Carpus*, about as long as propodus, smooth. *Propodus* (Fig. 4B) tergal surface irregular at widest point, with 1 simple seta midlength on sternal margin. *Fixed finger* with 1 distal seta on each margin and blunt process by insertion of distal tooth. *Dactylus* with 2 small spiniform setae on inner margin but without bifurcate process at distal tooth insertion. *Oostegites*. No ovigerous specimens found. *Pereopod 1* (Fig. 4C). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* smooth. *Merus* expanding in width distally, shorter than carpus, smooth. *Carpus* longer than dactylus and terminal spine together, with 1 distal simple seta. *Propodus* as long as carpus, with row of small tergal setae. *Dactylus* and terminal spine 0.5 propodus. *Pereopod 2* (Fig. 4D) similar to pereopod 1 except *ischium* with 1 sternal seta; *merus* with 1 sternal seta; *carpus* with 2 short sternal setae. *Pereopod 3* (Fig. 4E) resembles pereopod 2 except *carpus* with 2 longer sternal setae. *Pereopod 4* (Fig. 4F). *Basis* somewhat wider than 3 preceding pereopods, smooth. *Ischium* with 1 simple seta. *Merus* expanding in width distally, with 1 distal simple seta on tergal margin. *Carpus* longer than propodus, with 2 distal simple stout seta. *Propodus* with 3 distal simple stout setae. *Dactylus* and terminal spine marginally shorter than propodus. *Pereopod 5* (Fig. 4G) resembles pereopod 4 except *basis* tergal margin with 2 plumose setae; *merus* with 2 distal tergal setae; *carpus* with 3 distal stout simple setae; *propodus* with 3 distal simple stout setae and row of evenly spaced small simple setae on tergal margin; *dactylus* lost. *Pereopod 6* (Fig. 4H) similar to pereopod 4 except *basis* with 1 plumose seta; *ischium* smooth; *merus* with 2 setae; *carpus* with 3 distal simple stout setae; *propodus* with 3 distal stout setae and row of small setae; *dactylus* and terminal spine longer than propodus. *Pleopods* absent in females. *Uropods* (Fig. 3N) uniramous, uniarticulate and with 2 short and 2 distal long simple setae.

Description of male (Fig. 3C,D). *Pereon*. Pereonite 1 longer and narrower than female, shoulders less prominent. *Pleotelson* only marginally wider than pleon. *Pleopods* (Fig. 3F). All 5 pairs similar. *Exopod* and *endopod* armed with 8 simple setae on rami.

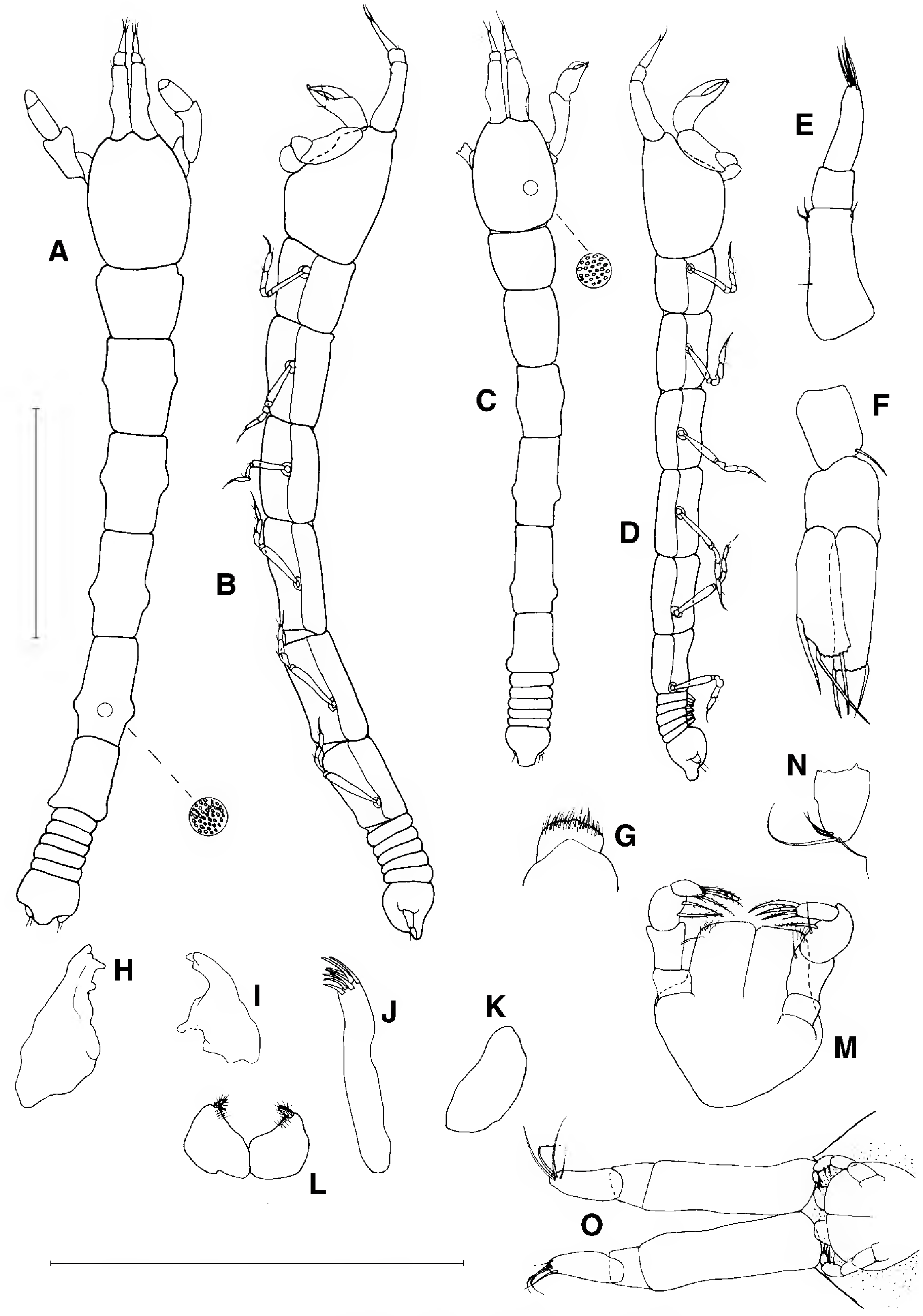


Figure 3. *Agathotanais ahyongi* n.sp., A, B & O, ♀ holotype AM P51007—A, dorsal view, scale bar = 1.0 mm; B, lateral view; O, cephalothorax, ventral view. *Agathotanais ahyongi* n.sp., C, D & F, juvenile ♂ paratype AM P51009—C, dorsal view; D, same lateral view; F, pleopod. *Agathotanais ahyongi* n.sp., E, G–N, ♀ paratype AM P51009—E, antennule; G, labrum; H, left mandible; I, right mandible; J, maxillule, palp not shown; K, maxilla; L, labium; M, maxilliped; N, uropod; scale bar for mouthparts = 0.25 mm.

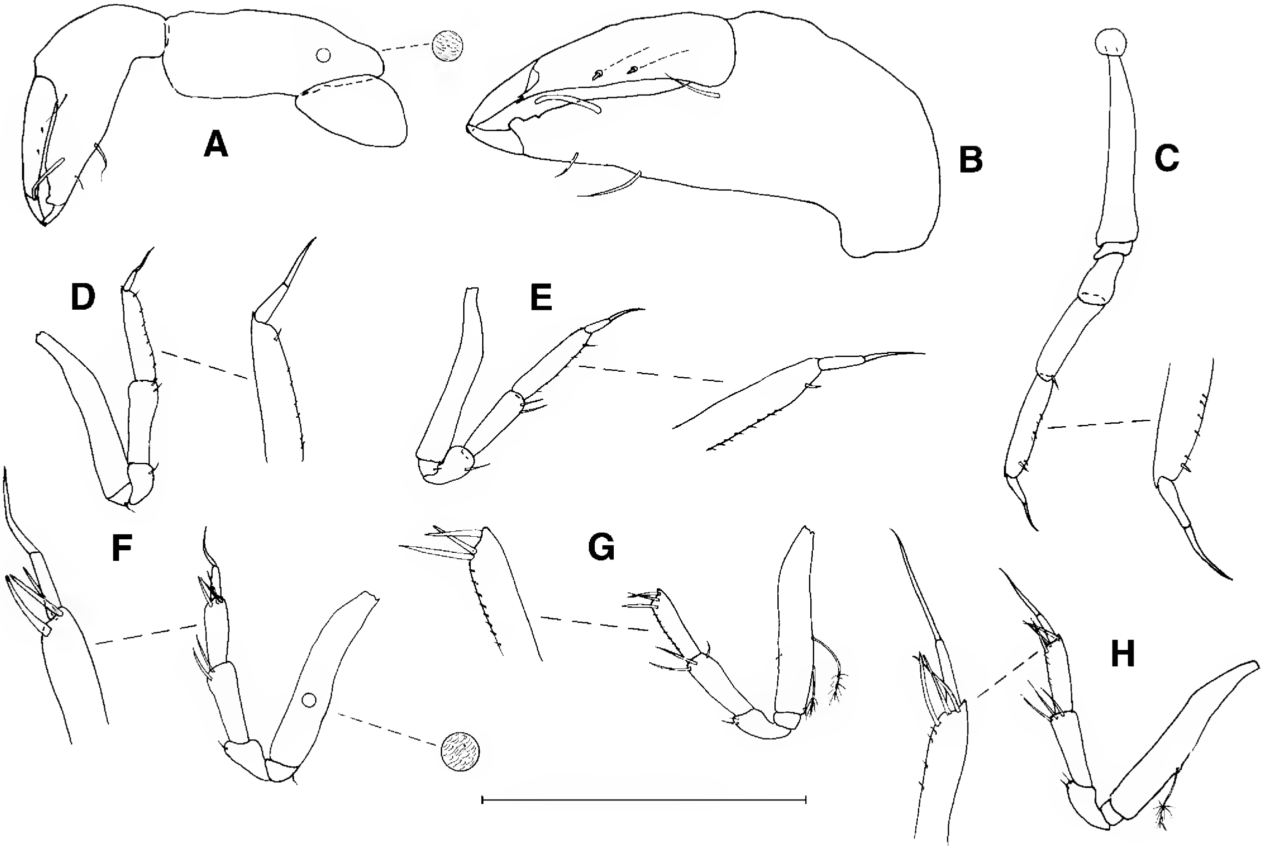


Figure 4. *Agathotanais ahyongi* n.sp., ♀ paratype AM P51009—A, cheliped; B, cheliped propodus and dactylus; C, pereopod 1; D, pereopod 2; E, pereopod 3; F, pereopod 4; G, pereopod 5; H, pereopod 6; scale bar = 0.3 mm.

Remarks. The reduction of the antenna to a lobe-like process reflects highest degree of reduction of this appendage within the Tanaidacea. The mouthparts of this species are significantly smaller than in other *Agathotanais* species.

Agathotanais spinipoda n.sp.

Material examined. HOLOTYPE (MV): 1 nonovigerous ♀ (body length 3.6 mm), slope station 69, MV J37856. PARATYPES (MV): 1 nonovigerous ♀, mouthparts and limbs dissected, slope station 27, MV J37880; 1 nonovigerous ♀, slope station 27, cut in two, mounted on SEM stub and coated, MV J37880.

Other material (MV). 26 nonovigerous ♀♀, 2 ♂♂, 11 juvenile ♀♀, 3 juvenile ♂♂, slope station 69; 1 nonovigerous ♀, 2 ♂♂, 1 manca II, slope station 32; 1 nonovigerous ♀, slope station 53; 1 ♂, slope station 33; 2 nonovigerous ♀♀, slope station 67; 10 nonovigerous ♀♀, 2 ♂♂, slope station 27; 8 nonovigerous ♀♀, 1 ♂, slope station 40.

Diagnosis. Antennule article 1 longer than rest of antennule. Antenna less than 0.3 times of antennule article 1 length. Pereopod 4–6 propodus with row of small spines. Pereonite 6 wider than long (l/w ratio 0.9). Uropods not extending beyond pleotelson apex.

Etymology. Name refers to the unusual spines on the propodus and carpus of pereopods 4–6.

Description of adult female (Fig. 5A,B). *Body* cylindrical, stout. *Cephalothorax* (Fig. 5G) shorter than first 2 pereonites, anterolateral corners slightly concave. *Pereonites*. Pereopod shoulders are placed anteriorly on pereonite 1, midlength on pereonites 2–4 and posteriorly on pereonites 5 and 6. *Pereonite 1* wider than long, l/w ratio 0.6, shorter than other pereonites. *Pereonite 2–6* l/w ratio 0.7, 0.85, 0.95, 1.05, 0.9. *Pleon*. *Pleonites* of similar size, narrower than pereon and pleotelson. *Pleotelson* as long as last 2 pleonites together, apex margin straight. *Antennule* (Fig. 5E) with 3 articles. *Article 1* twice as long as rest of antennule, with 2 simple setae midlength and 4 distally. *Article 2* 0.5 times article 3 length, with 1 distal thick seta. *Article 3* with at least 2 distal long setae. *Antenna* (Fig. 5F) uniarticulate, less than 0.3 times antennule article 1, with row of small setae. *Mouthparts*. *Labrum* (Fig. 6A), distal margin with small medial lobe, setose. *Left mandible* (Fig. 6B) incisor bifurcate, lacina consists of tiny lobe only. *Right mandible* (Fig. 6C) incisor consists of 1 blunt tooth. *Labium* (Fig. 6D) with anterolateral processes and plumose spiniform seta midlength. *Mandibles* molar process consisting of membranous lobe only. *Maxillule* (Fig. 6E)

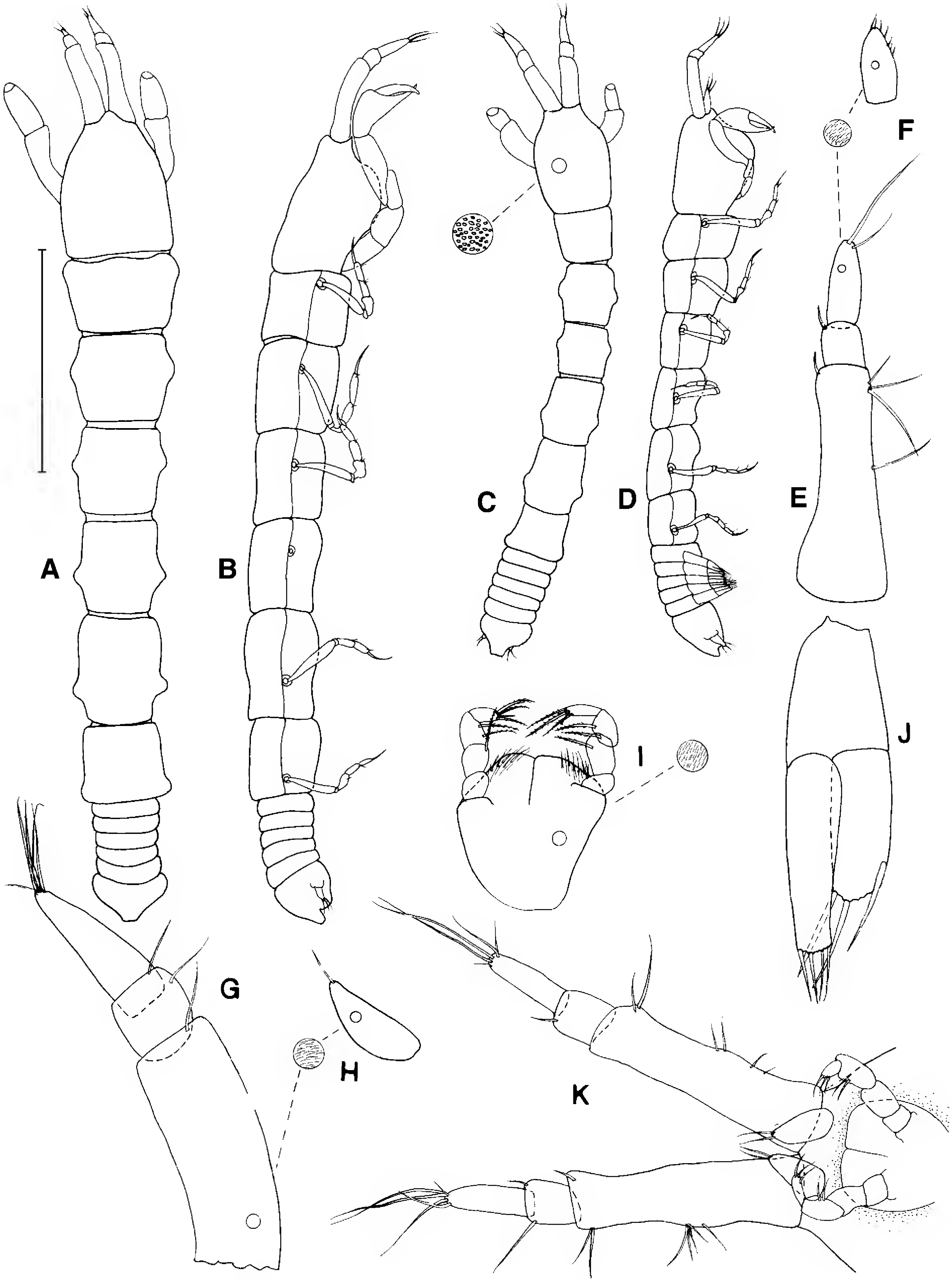


Figure 5. *Agathotanais spinipoda* n.sp., A, B & K, ♀ holotype MV J37856; C, D, G–J, ♂ paratypes, and E, F, ♀ paratype, MV J37880. A, ♀ dorsal view, scale bar = 1.0 mm. B, same lateral view; C, ♂ dorsal view; D, same lateral view; E, ♀ antennule; F, ♀ antenna; G, ♂ antennule; H, ♂ antenna; I, ♂ maxilliped; J, pleopod; K, cephalothorax, ventral view.

endite with 7 distal thick setae; palp broken off. *Maxilla* (Fig. 6F) extremely elongate with no discernible features. *Maxilliped* (Fig. 6G) basis fused medially. Endites with proximal lobes and more heavily setose on anterolateral corners. Palp article 1 outer margin longer than inner, smooth; article 2 inner margin longer than outer and with 3 distal setae; article 3 with 3 setae on inner margin; article 4 with 4 distal setae. *Epignath* (Fig. 6H) with distal setules. *Cheliped* (Fig. 7G). *Basis* rectangular, less than half the length of carpus. *Merus* with 1 simple seta sternally. *Carpus* subequal to propodus, with 1 simple seta midlength and 1 distally on each margin. *Propodus* (Fig. 7H) tergal surface uneven at widest point, with 1 simple seta midlength on sternal margin and 1 by dactylus insertion. *Fixed finger* with 2 distal setae on inner margin and pointed process by insertion of distal tooth. *Dactylus* with bifurcate process next to insertion of distal tooth and 2 small spiniform setae on inner margin. *Oostegites*. No ovigerous specimens found. *Pereopod 1* (Fig. 7A). *Basis* longer than next 3 articles together, setulate but otherwise smooth. *Ischium* with 1 distal simple seta on tergal margin. *Merus* expanding in width distally, shorter than carpus, with 2 distal simple setae on tergal margin. *Carpus* shorter than dactylus and terminal spine together, with 1 distal simple seta on each margin. *Propodus* 0.3 times longer than carpus, with 1 distal simple seta and denticulate scale. *Dactylus* and terminal spine as long as propodus. *Pereopod 2* (Fig. 7B) similar to pereopod 1 except *merus* smooth, *propodus* with 1 distal short spine on sternal margin. *Pereopod 3* (Fig. 7C) similar to pereopod 1 except *carpus* with 2 distal setae on tergal and 1 on sternal margin. *Pereopod 4* (Fig. 7D). *Basis* somewhat wider than on other pereopods; tergal margin with 2 plumose setae sternally with 1 simple seta. *Ischium* band shaped with 2 distal simple setae. *Merus* expanding in width distally, with 2 distal simple setae on tergal margin. *Carpus* as long as propodus, with 1 simple stout seta distally and 3 short spines on tergal margin. *Propodus* with 3 distal simple stout setae and 5 short spines on tergal margin. *Dactylus* and terminal spine longer than propodus and weakly setulate. *Pereopod 5* (Fig. 7E) similar to pereopod 4 except *basis* tergal margin with 2 plumose setae, *propodus* with 3 tergal spines, *dactylus* and terminal spine appear smooth. *Pereopod 6* (Fig. 7F) similar to pereopod 4 except *basis* without plumose setae, *merus* with 1 seta only, *carpus* with 1 distal simple stout seta and 2 short spines on tergal margin, *propodus* with 3 distal stout setae and 3 short spines on tergal margin, *dactylus* and terminal spine appear smooth. *Pleopods* absent in females. *Uropods* (Fig. 7I) uniramous, uniarticulate and with 3 long and 1 short simple and 1 distal plumose seta and 1 simple and plumose setae at point of narrowing. Long simple seta on exopod process.

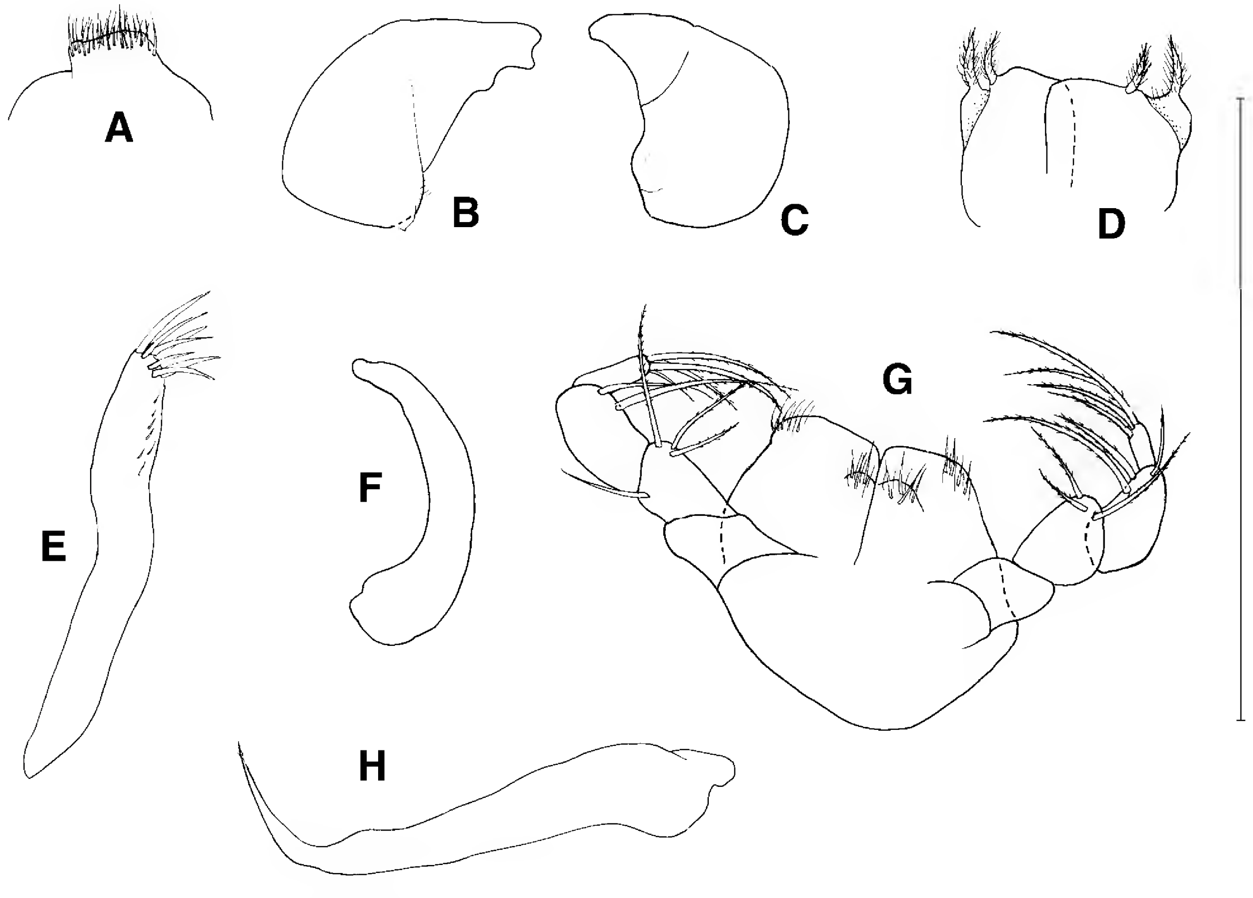


Figure 6. *Agathotanais spinipoda* n.sp., ♀ paratype MV J37880—A, labrum; B, left mandible; C, right mandible; D, labium; E, maxillule, palp not shown; F, maxilla; G, maxilliped; H, epignath; scale bar = 0.25 mm.

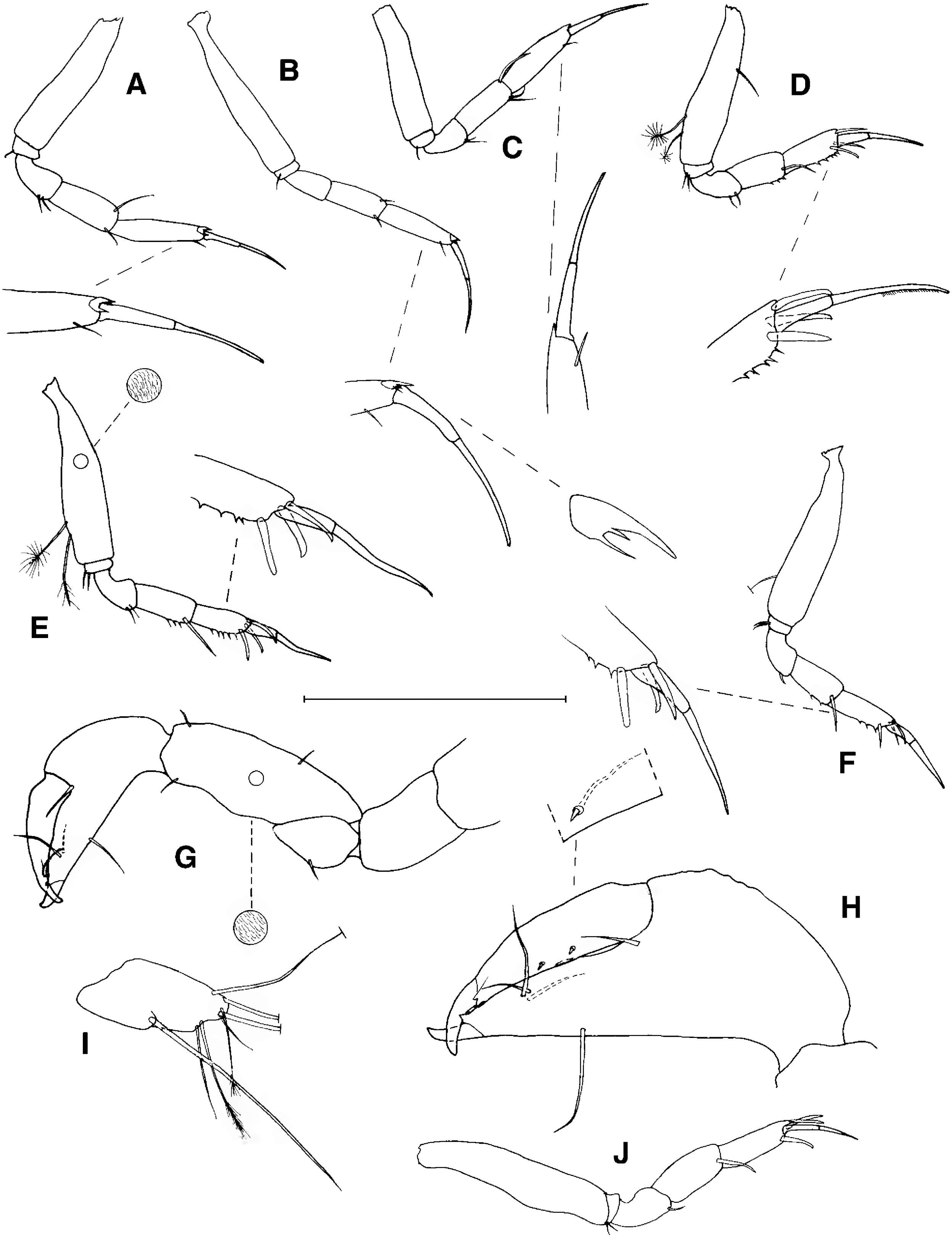


Figure 7. *Agathotanais spinipoda* n.sp., A–I, ♀ paratype MV J37880. A, pereopod 1; B, pereopod 2; C, pereopod 3; D, pereopod 4; E, pereopod 5; F, pereopod 6; G, cheliped; H, cheliped propodus and dactylus; I, uropod; J, ♂ pereopod 5; scale bar = 0.3 mm.

Description of male (Fig. 5C,D). *Pereon.* Pereopod 1 longer and narrower than that of female, shoulders less prominent. *Pleotelson* not wider than pleon. *Maxilliped* (Fig. 5I) smaller than female and endites without proximal lobes. *Antennule* (Fig. 5G) thicker and longer than in female (more than 0.25 times), with distal aesthetasc. *Antenna* (Fig. 5H) 0.5 times longer than female antenna. *Pereopods* (Fig. 7J) without propodus spines. *Pleopods* (Fig. 5J). All 5 pairs similar, *exopod* armed with 8 and *endopod* with 7 simple setae on rami.

Remarks. A common species on the southeast Australian slope at bathyal depths (400–1840 m). The tubes made of mud sediment particles and a few sponge spicules. *Agathotanais spinipoda* n.sp. shares the pereopod 4–6 spine character with *A. ghilarovi* but can be distinguished from it by the lack of maxilliped endite denticles, by the broad antennule and longer antennule article 1.

Agathotanais sp. incertae sedis

Material examined. 1 nonovigerous ♀, DOMES site A station DJ41; 1 manca, DOMES station DJ15. Additional material originally identified as *Agathotanais hanseni*, are possibly also this species but the poor condition of the specimens does not allow confirmation; 2 nonovigerous ♀♀, 1 fragment, USAP station 3, "Chilii Trench", 16°12'S 74°41'W, 2599–5858 m; 2 nonovigerous ♀♀, USAP station 12, Taomin Sea, 40°00.42'S 153°00.03'W, 4564 m.

This species is not described because only one adult specimen is available. It is, however, easily distinguished from the other species of *Agathotanais* by the pleotelson apex being sharply pointed.

Key to species of the genus *Agathotanais*

1 Antenna absent .... *A. ahyongi* n.sp.

—— Antenna present 2

2 Antenna consisting of 2 articles .... *A. manganicus* n.sp.

—— Antenna uniarticulate 3

3 Pereopod 4 propodus with tergal row of small spines 7

—— Pereopod 4 propodus without tergal row of small spines 4

4 Pereonites 4 + 5 wider than long. Carapace as long as pereonites 1 + 2 together .... *A. brevis**

—— Pereonites 4 + 5 longer than wide or subequal. Carapace shorter than pereonites 1 + 2 together 5

5 Pereonites 4 + 5 subequal in length and width .... *A. ingolfi*

—— Pereonites 4 + 5 longer than wide 6

6 Pleon narrower than pereon .... *A. hanseni*

—— Pleon as wide as pereon .... *A. splendius**

7 Antennule article 1 almost 3 times longer than article 3. Maxilliped endites without caudodistal denticles .... *A. spinipoda* n.sp.

—— Antennule article 1 only 1.5 times longer than article 3. Maxilliped endites with caudodistal denticles .... *A. ghilarovi**

* Specimens of *Agathotanais splendius, A. ghilarovi* and *A. brevis* could not be obtained and key characters are taken from the original descriptions only.

Discussion

Sieg (1983) stated that *Agathotanais* is defined by apomorphic characters but without direct references to which. Sieg (1983) did, however, claim that most reductions within the Tanaidacea are apomorphic character trends. If this is true, then the apomorphic characters are: 3-articulated antennule, rudimentary antenna, reduction of adult male mouthparts and absence of uropodal exopod. A preliminary phylogenetic analysis using the Apseudomorpha, Neotanaidomorpha and *Tanais* as outgroups, supports this view and suggests that the other diagnostic features (i.e. ventral cheliped attachments, heavily calcified cuticle, labial processes, modified male pleopods) are also apomorphic trends, while the limited sexual dimorphism is a pleisiomorphic character (Larsen, research in progress).

Within *Agathotanais* the above mentioned reductions vary considerably. The long, 2-articulated antenna of *A. manganicus* n.sp. may represent a plesiomorphic character state, approaching that of the *Paragathotanais* and *Paranarthrura*. The reduction of the antenna to a lobe-like structure in *A. ahyongi* n.sp. may represent an apomorphic trend. *Agathotanais ahyongi* also displays a loss of median plumose seta on the labium, otherwise thought to be an apomorphic generic character. The reduction of male mouthparts have long been considered an apomorphic trend (Sieg, 1986). This reduction is closely coupled to sexual maturity (Lang, 1953). As seen in *A. spinipoda* n.sp., juvenile male *A. spinipoda* (defined by the incompletely developed pleopods) did have a complete set of mouthparts, resembling, but not identical to, those of the adult female. Males with completely developed pleopods retain only a small maxilliped and the epignath.

Agathotanais as currently defined, is a cosmopolitan genus, found in the northeast- and northwest Atlantic, southeast Atlantic, Central American Pacific slope, mid- and northeast Pacific, the eastern slope of Australia and in the Indian Ocean. This distribution pattern is similar to that of most tanaid genera. So far, extensive new Pacific/Australian material has revealed only one genus (*Bathytanais*), which appears to have a distribution restricted to the Australian region. Tanaids may thus follow the distribution patterns of amphipods and cumaceans in the deep sea and not those of isopods (Hessler & Wilson, 1983).

ACKNOWLEDGMENTS. Financial support for this research was provided by the Danish Research Academy. I am grateful to my supervisor Dr G.D.F. Wilson (AM), and my co-supervisor Dr N.N. Tait (MQ), for their support. Thanks to Dr W. Ivantsoff (MQ) for translating the Russian text. I also thank Drs P. Berents (AM), J. Cordeiro (AMNH), D.E. Jacobsen (ZMUC) and E. Wallis (MV), for loan of specimens. The DOMES site A specimens were collected during the tenure of US National Oceanographic and Atmospheric Administration contract to Dr P.A. Jumars, University of Washington.

References

Barnard, K.H., 1920. Contribution to the crustacean fauna of South Africa. 6. Further additions to the list of marine Isopoda. *Annals of the South African Museum* 17: 319–438.

Beklemischew, W.N., 1958. Grundlagen der Vergleichende Anatomie der Wirrellosen. I. Promorphologie. Berlin: Deutsher Verlag der Wissenschaften.

Bird, G.J., & D.M. Holdich, 1988. Deep-sea Tanaidacea (Crustacea) of the north-east Atlantic: the tribe Agathotanais. *Journal of Natural History* 22: 1591–1621.

Bird, G.J., & D.M. Holdich, 1989. Deep-sea Tanaidacea (Crustacea) of the north-east Atlantic: the genus *Paranarthrura* Hansen. *Journal of Natural History* 23: 137–167.

Gardiner, L.F., 1975. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contributions to Zoology* 170: 1–265.

Hansen, H.J., 1913. Crustacea, Malacostraca. II. *Danish Ingolf Expedition* 3: 1–127.

Hessler, R.R., & G.D.F. Wilson, 1983. The origin and biogeography of malacostracan crustaceans in the deep sea. In *Evolution in Time and Space: The Emergence of the Biosphere*, eds. R.W. Sims, J.H. Price and P.E.S. Whally, pp. 227–254. London & New York: Academic Press.

Kornicker, L.S., & G.C.B. Poore, 1996. Ostracoda (Myodocopina) of the SE Australian Continental Slope, Part 3. *Smithsonian Contributions to Zoology* 573: 1–186.

Kudinova-Pasternak, R.K., 1970. Tanaidacea of the Kuril-Kamchatka Trench. *Trudy Instituta Okeanologii. Akademiya Nauk SSSR* 86: 341–380.

Kudinova-Pasternak, R.K., 1989. Tanaidaceés Abyssales (Crustacea, Tanaidacea) Des Parties Nord-Est et Centrale de l'Ocean Indien (d'Aprés des Matériaux de l'Expedition Francaise "Safari-II") 2. Sous-Ordre Tanaidomorpha. *Zoologicheskii Zhurnal* 68(3): 27–40.

Kudinova-Pasternak, R.K., 1990. Tanaidacea (Crustacea, Malacostraca) of Southeastern part of Atlantic Ocean and the region to the north off Mordvinov (Elephant) Island. *Trudy Instituta Okeanologii. Akademiya Nauk SSSR* 126: 90–107.

Lang, K., 1949. Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologi* 42(18): 1–14.

Lang, K., 1953. The postmarsupial development of the Tanaidacea. *Arkiv för Zoologi* 2(4): 409–422.

Lang, K., 1968. Deep-sea Tanaidacea. *Galathea Reports* 9: 23–209.

Lang, K., 1971a. Taxonomische und phylogenetische untersuchungen über die Tanaidaceen. 6. Revision der gattung *Paranarthrura* Hansen, 1913 und aufstellung von zwei neuen familien, vier neuen gattungen und zwei neuen arten. *Arkiv för Zoologi* 2(23): 361–401.

Lang, K., 1971b. Die Gattungen *Agathotanais* Hansen und *Paragathotanais* n.gen. (Tanaidacea). *Crustaceana* 21: 57–71.

Larsen, K., 1999. Deep-Sea Tanaidaceans from the Albatross cruises 1885–86 with keys to the Neotanaidomorpha. *Journal of Natural History*, in press.

Larsen, K., & G.D.F. Wilson, 1998. Tanaideomorphan systematics—is it obsolete? *Journal of Crustacean Biology* 18(2): 346–362.

Nierstrasz, H.F., 1913. Isopoda Chelifera. *Siboga Expeditie* 32a: 1–56.

Poore, G.C.B., 1994. Marine biogeography of Australia. In *Marine Zoology of Australia*, eds. L.S. Hammond & R. Synnott, pp. 336–357. Melbourne: Longman Cheshire.

Poore, G.C.B., J. Just & B. Cohen, 1994. Composition and diversity of Crustacea Isopoda of the southeastern Australian continental slope. *Deep Sea Research* 41: 677–693

Poore, G.C.B., & G.D.F. Wilson, 1993. Marine species richness. *Nature* 361: 597–598.

Shiino, S.M., 1952. A new genus and two new species of the order Tanaidacea found at Seto. *Publications from the Seto Marine Biological Laboratory* II(2): 53–68.

Sieg, J., 1973. *Ein Beitrag zum Natürlichen System der Dikonophora Lang*. Unpublished thesis, University of Kiel, pp. 298.

Sieg, J., 1976. Zum natürlichen system der Dikonophora Lang (Crustacea, Tanaidacea). *Zeitschrift für Zoologischer Systematik und Evolutionsforschung* 14: 177–198.

Sieg, J., 1980. Sind die Dikonophora eine polyphylogenetishe gruppe? *Zoologischer Anzieger* 205: 401–416.

Sieg, J., 1983. Evolution of Tanaidacea. In *Crustacean Issues 1, Crustacean Phylogeny*, ed. F.R. Schram, pp. 229–256. Rotterdam.

Sieg, J., 1986. Tanaidacea (Crustacea) von der Antarktis und Subantarktis. II. Tanaidacea gesammelt von Dr. J.W. Wägele während der Deutschen Antarktis Expedition 1983. *Mitteilungen aus der Zoologischen Museum der Universität Kiel* 2(4): 1–80.

Thistle, D., & G.D.F. Wilson, 1987. A hydrodynamically modified, abyssal isopod fauna. *Deep Sea Research* 34: 73–87.

Zimmer, C., 1926. Northern and Arctic invertebrates in the collection of the Swedish State Museum X: Cumaceen. *Kungliga Svenska vetenskabsakdemiens handlinger* 3(2): 1–88.

Manuscript received 9 April 1998, revised 24 November 1998 and accepted 4 January 1999.

Associate Editor: G.D.F. Wilson.

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 113–122. ISSN 0067-1975

A New Genus and Two New Species of Myrophine Worm-eels, with Comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae)

P.H.J. CASTLE [1] AND JOHN E. MCCOSKER [2]

[1] School of Biological Sciences, Victoria University of Wellington,
PO Box 600, Wellington 6000, New Zealand
peter.castle@vuw.ac.nz

[2] California Academy of Sciences, Golden Gate Park,
San Francisco, CA 94118, United States of America
jmccosker@calacademy.org

ABSTRACT. *Skythrenchelys* n.gen. differs from other myrophine ophichthids in the condition of its gill openings (moderately elongate and below lateral midline), dentition (large, conical and uniserial), posterior nostril (entirely outside mouth), and other characters. *Skythrenchelys zabra* n.sp., the type species, is described from India, the Philippines, Indonesia and northern Australia; *S. lentiginosa* n.sp. is described from the Red Sea. *Scolecenchelys* Ogilby, previously a subgenus of *Muraenichthys* Bleeker, is generically distinct on the basis of differences in dentition (teeth conical and uniserial or biserial *vs* blunt and multiserial), cephalic pores (2 pores between anterior and posterior nostrils *vs* 1 pore), and its posterior nostril condition (within *vs* outside mouth). Valid species of *Muraenichthys* and *Scolecenchelys* and their synonyms are identified.

CASTLE, P.H.J., & JOHN E. MCCOSKER, 1999. A new genus and two new species of myrophine worm-eels, with comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae). *Records of the Australian Museum* 51(2): 113–122.

The most recent revision of the snake-eel and worm-eel family Ophichthidae (McCosker *et al*., 1989) recognised 55 genera, including 44 in the Subfamily Ophichthinae and 11 in the Myrophinae. The family is worldwide in distribution, principally but not exclusively in inshore waters of tropical seas. Its members mainly live burrowed tail first in soft sediments and readily avoid capture by most sampling methods, though they are variously vulnerable to ichthyocides. This may explain why some of the approximately 250 ophichthid species are known from few or even single specimens. Ophichthids have distinctive leptocephali, many of which were documented in the Atlantic by Leiby (1989), though most have not yet been identified.

The comprehensive treatment of the Ophichthidae by McCosker *et al.* (1989) brought together what is known of the western North Atlantic species in this family. In contrast, the ophichthid fauna of the Indo-west Pacific is much less well known. Localities where soft sediments of coral sand to mud predominate occur widely but are poorly sampled and warrant further attention. It is expected that new ophichthid taxa will be found from time to time in the Indo-west Pacific, as evidenced by recent records and by those reported here. This paper describes a new genus and two new species of myrophine worm-eels from such habitats, and reviews the related genera *Muraenichthys* Bleeker, 1853 and *Scolecenchelys* Ogilby, 1897.

The worm-eels of the subfamily Myrophinae comprise approximately 55 species distributed among 11 genera. The majority have been uncomfortably assigned to the genera *Myrophis* Lütken, 1851 (seven to eight species), *Pseudomyrophis* Wade, 1946 (eight species), and *Muraenichthys* (about 25 species) in that they lack characters so outstanding as to allow recognition of monophyletic lineages. In his treatment of the osteology and relationships of the Ophichthidae, McCosker (1977) identified subgeneric lineages within *Muraenichthys* but was hesitant to recognise them at the generic level pending a more thorough analysis of the species within that complex assemblage.

Several years ago we were provided with specimens of two remarkable new species, described herein, whose affinities were clearly with *Muraenichthys* (sensu lato). However, we were reluctant to describe them within that genus because of their unique physiognomy and associated characters. After the examination of specimens of most of the Tribe Myrophini, we are now confident in describing them as species of a new genus and at the same time separating two lineages within *Muraenichthys*. In particular, we herein elevate the subgenus *Scolecenchelys* to generic rank. This work is not meant to be a revisionary study of either genus in that numerous problems remain concerning the limits of species which we therefore conservatively retain.

Methods

Measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length, body length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; maximum body depth does not include the median fins. Head pore terminology follows that of McCosker *et al.* (1989) such that the supraorbital pores (SO) are expressed as the ethmoid pore + pores in supraorbital canal, e.g., 1 + 3; infraorbital pores (IO) are expressed as pores along the upper jaw + those in vertical part of canal behind eye (the "postorbital pores"), e.g., 4 + 1, in that the last pore included along the upper jaw is part of the postorbital series; the preoperculomandibular pores (POM) include those along the lower jaw and those on the preopercular canal; the supratemporal pores (ST) include those on the dorsolateral side of the head in front of the lateral line pores. The median frontal and supratemporal pores are not included since they are present in all specimens examined. We are not fully satisfied that the numbers of POM pores and our interpretation of them that we have given is definitive. For example, the 6th mandibular pore may well be the first of the preopercular series, such is the extent of posterior displacement of the jaw angle; also, the stained paratype of *S. zabra* n.sp. (CAS 99802) shows just 2 pores in the preopercular series, confirmed in the unstained CAS specimen, while the NMNZ holotype and 2 paratypes apparently have 3 preopercular pores. Osteological examination involved clearing and counterstaining with alcian blue and alizarin red dyes (Dingerkus & Uhler, 1977). Vertebral counts (which include the hypural) were taken from radiographs. Radiographic techniques are described in Böhlke (1989). The mean vertebral formula (MVF) is expressed as the average of predorsal, preanal, and total vertebrae (Böhlke, 1982). Institutional abbreviations used in the text and figures are as listed in Leviton *et al.* (1985). All material is deposited in one or other of the above institutions, as indicated in the text.

AMS	Australian Museum, Sydney
BPBM	Bernice P. Bishop Museum, Honolulu
CAS	California Academy of Sciences, San Francisco
MNHN	Muséum national d'Histoire naturelle, Paris
NMNZ	National Museum of New Zealand, Wellington
NTM	Northern Territory Museum, Darwin
SIO	Scripps Institution of Oceanography, La Jolla, USA
USNM	United States National Museum, Washington D.C.

Skythrenchelys n.gen.

Type species. *Skythrenchelys zabra* n.sp.

Material examined. Holotypes and paratypes of *S. zabra* n.sp. and *S. lentiginosa* n.sp. Cleared and stained material: paratype of *S. zabra* n.sp., CAS 99802, TL 282 mm; *Muraenichthys gymnopterus* (Bleeker, 1853), CAS 61117, TL 184 mm; CAS 98928, TL 242 mm; SIO 69-276, TL 144 mm; *M. schultzei* Bleeker, 1857, CAS 35587, TL 176 mm; paratype of *Scolecenchelys chilensis* (McCosker, 1970), SIO 65-645, TL 248 mm; *S. gymnotus* (Bleeker, 1857), CAS 64946, TL 249 mm; SIO 69-266, TL 244 mm; *S. macropterus* (Bleeker, 1857), SIO 69-277, TL 181 mm.

Diagnosis. Elongate myrophines, Tribe Myrophini (*sensu* McCosker, 1977), with tail equal to or shorter than head and trunk, laterally compressed posteriorly. Snout conical, its underside not grooved and extending just beyond tip of lower jaw. Anterior nostril in a short tube that does not extend beyond lip; posterior nostril a hole with a small anterior flap, entirely above margin of upper lip, slightly below and in advance of orbit. Jaws elongate, centre of orbit in advance of middle of upper jaw. Lips smooth, without crenulae or barbels. Gill opening below lateral midline, unconstricted and elongate for a myrophine, nearly equal in length to isthmus. Median fins low but apparent; dorsal fin origin along trunk or above anus. Pectoral fins absent or a minute remnant. Cephalic and lateral line pores developed; supraorbital, frontal, infraorbital, preoperculo-mandibular and supratemporal pore (including median supratemporal) series present; lateral line pores absent from posterior third of tail. Teeth conical and large, uniserial on jaws and vomer. Gill arches not well developed; upper pharyngeal tooth plates closely sutured but not fused. Neurocranium stout, sub-truncate posteriorly, supraoccipital crest barely developed. Jaws elongate, suspensorium posteriorly inclined, about 60° to horizontal; maxillae elongate and tapering posteriorly. Opercle and preopercle developed, other elements cartilaginous or absent. Branchiostegal rays typically myrophine (*sensu* McCosker, 1977), 6 attached to outer face of each epihyal with 32 unattached pairs well behind the basal arch. Pectoral girdle reduced to stout cleithrum and thin supracleithrum. Epipleural ribs on all precaudal vertebrae. Other characters those of the two species.

Distribution. Known from two species, ranging from the Red Sea and the Indian and western Pacific oceans, respectively.

Etymology. From Greek *skythros* (angry or sullen) and *enchelys* (an eel), in reference to the facial expression of the two included species. Treated as feminine according to Opinion 95 of the *Bulletin of Zoological Nomenclature*, 1970.

Affinities of the genus. The species of *Skythrenchelys* n.gen. are unique within the Myrophini in the conditions of their gill opening size and location, their dentition, and the inclination of the suspensorium and associated elongation of the jaws. They share with species of *Muraenichthys* the condition of their posterior nostril and the presence of but one supraorbital pore between the anterior and posterior nostrils. As well, *Skythrenchelys* n.gen. and *Muraenichthys* are more similar to each other in certain osteological characters (note: this analysis is based on the osteological preparation of *S. zabra* n.sp.; the single, small specimen of *S. lentiginosa* n.sp. only allowed radiographic examination) such as the slender supracleithrum, stout cleithrum, and the general shape of the neurocranium, than to those of other myrophines. The species of *Skythrenchelys* further differ from all other myrophines in the characters listed in the Key and in Table 1.

Upon cursory examination, the species of *Skythrenchelys* n.gen. are obviously myrophine in appearance, and could be mistaken for certain species of *Scolecenchelys*. The condition of the elongate jaw and the enlarged dentition are unique, and will differentiate them from any other myrophine.

Table 1. Characteristics of the genera *Skythrenchelys* n.gen., *Muraenichthys* and *Scolecenchelys*. IOP = infraorbital pore between anterior and posterior nostrils; POP^3 = third preopercular pore.

character	*Skythrenchelys* n.gen.	*Muraenichthys*	*Scolecenchelys*
gill opening	unconstricted	constricted	constricted
centre of orbit	before mid-jaw	» mid-jaw	behind mid-jaw
dentition	conical, mostly uniserial	blunt, multiserial	conical, uniserial or biserial
posterior nostril	in outer lip, with a small flap	in outer lip, with a prominent flap	inside of or along lip
POP^3	present or absent	present or absent	present
IOP	1	1	2

Key to the genera of Myrophinae lacking pectoral fins

1 Gill opening along lateral midline, a constricted opening; posterior nostril opening either along upper lip and preceded by a flap, within the mouth and covered by a flap, or entirely within the mouth; teeth varying from conical to blunt, uniserial to multiserial, all smaller than width of orbit 2

—— Gill opening more or less below lateral midline, unconstricted, its length about equal to interbranchial; posterior nostril opening entirely outside of mouth, a hole along upper lip preceded by a small flap; teeth conical and uniserial, the largest as long as the width of the orbit .... *Skythrenchelys* n.gen.

2 Posterior nostril opens into mouth, covered partially or entirely by an exterior flap; 2 pores between nostrils; jaw teeth usually conical, uniserial or biserial, intermaxillary teeth not in a broad patch 3

—— Posterior nostril opening outside of mouth, a hole along upper lip preceded by a flap; 1 pore between anterior and posterior nostrils; teeth blunt, jaw teeth in bands; intermaxillary teeth in a patch ....*Muraenichthys* Bleeker, 1853

3 Tongue not elongate, not extending outside of mouth, and lacking a fleshy appendage at its tip; inner edge of lips and palate smooth; teeth either conical or small and villiform, uniserial or multiserial 4

—— Tongue elongate, extending well beyond mouth and decorated with a fleshy appendage; inner edge of lips and palate decorated with fleshy lappets; teeth conical and uniserial .... *Glenoglossa* McCosker, 1982

4 Ventral side of snout without a prominent median groove bordered by dermal folds; anterior nostrils less than eye in length 5

—— A prominent median toothed groove on ventral side of snout, bordered by dermal folds, extending anteriorly to anterior nostrils; anterior nostrils elongated tubes equal to eye in length .... *Schismorhynchus* McCosker, 1970

5 Teeth absent on vomer, absent or embedded on intermaxillary, those on maxillary and dentary minute or villiform; dorsal-fin origin behind anus .... *Schultzidia* Gosline, 1951

—— Teeth present on intermaxillary, maxillary, dentary and vomer; dorsal-fin origin either before or behind anus .... *Scolecenchelys* Ogilby, 1897.

Skythrenchelys zabra n.sp.

Figs. 1A–C, 2A; Table 2

Material examined. HOLOTYPE: female, TL 239 mm, Thevara, Ernakulam, southern India, 10°00'N 76°16'E, shallow, turbid water, K.H. Mohamed, 18 July 1956, NMNZ 35152. PARATYPES: TL 234–280 mm (2), same data as holotype, NMNZ 35153; TL 256–269 mm (2, the larger cleared and stained), same data as holotype, CAS 99802; TL 259 mm (1), same data as holotype, AMS 38844-001; TL 234 mm (1), same data as holotype, BPBM 38404; TL 185 mm (1), north of Smith Point, Cobourg Peninsula, Northern Territory, Australia, 12°58'S 132°10'E, prawn trawl by N.R. Anson, 18 October 1981, NTM S.10031-004; TL 296 mm (1), Manila Bay, MUSORSTOM-Philippines 1976, station 2, trawled in 180 m, 19 March 1976, MNHN 1998-681; TL 133 mm (1), Iloilo, Panay Island, Philippine Islands, H.C. Kellers, 20 March 1929, USNM 148574; TL 119 mm (1), Straits of Malacca, 08°10'N 92°00'E, W. Gladfelter, November–December 1961, USNM 193227.

Diagnosis. A moderately elongate species of *Skythrenchelys* n.gen. with the following characters: tail 43–46% of TL; dorsal fin arising in mid-trunk; head pores: SO 1 + 4, IO 4 + 1, POM 6 + 2 or 3, ST 2; teeth conical, prominent, uniserial in jaws and on vomer; colour uniform tan. Mean vertebral formula 33.4/56.7/118.6.

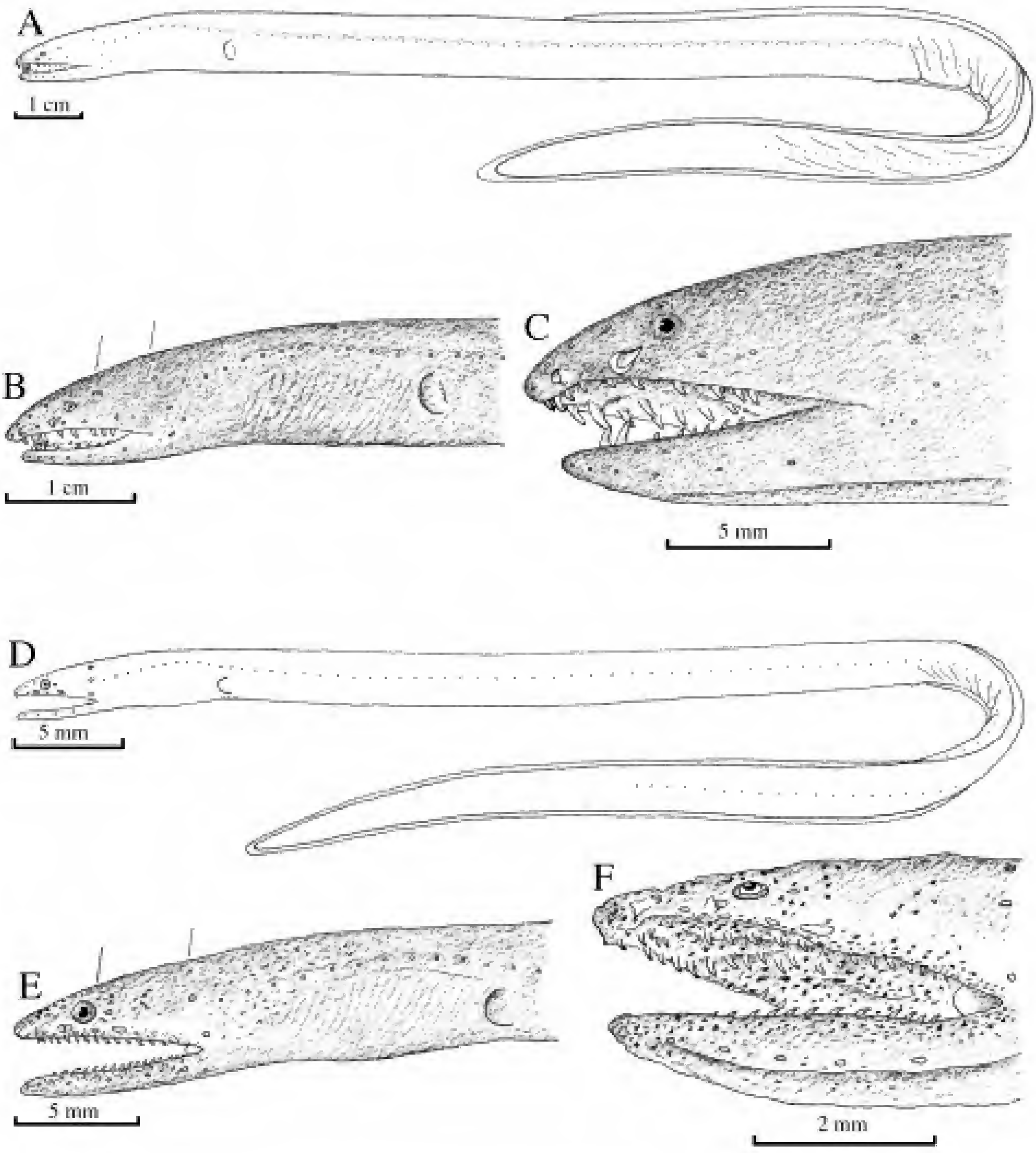


Figure 1. A–C, *Skythrenchelys zabra* n.sp., holotype, NMNZ 35152, TL 239 mm; A, body, lateral view; B, head, frontal and median supratemporal pores indicated; C, anterior part of head, ventrolateral to show intermaxillary, vomerine, maxillary and dentary teeth. D–F, *S. lentiginosa* n.sp., holotype, BPBM 29320, TL 165 mm; D, body, lateral view; E, head, median pores indicated; F, anterior part of head, ventrolateral to show intermaxillary, vomerine, maxillary and dentary teeth.

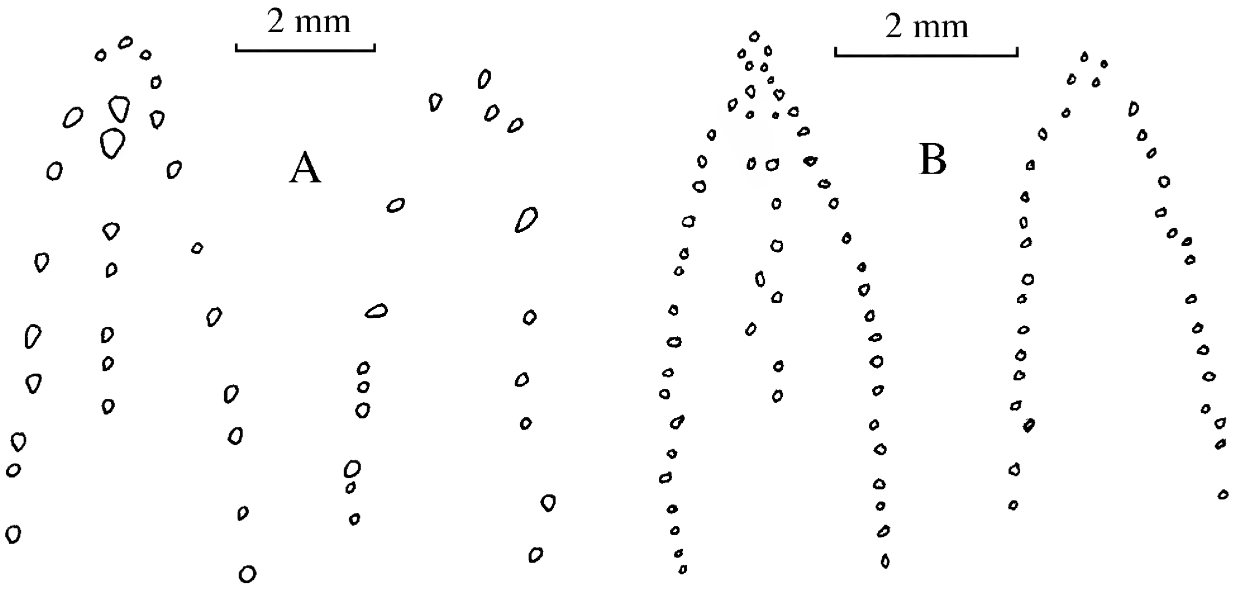


Figure 2. Patterns of upper (left) and lower (right) dentition of A—*Skythrenchelys zabra* n.sp., paratype, NTM S.10031-004, TL 185 mm; and B—*S. lentiginosa* n.sp., holotype, BPBM 29320, TL 165 mm. The sketches show arrangement, number and general size of the teeth, not their shape.

Further description. Measurements of holotype in mm. Total length 239; head length 31.9; trunk length 100.6; tail length 106.5; body depth at gill opening 8.9; body width at gill opening 4.5; body depth at anus 8.3; origin of dorsal fin 80.5; gill opening length 3.9; gill opening interspace 4.5; snout length 4.1; upper jaw length 9.0; eye diameter 1.0; interorbital space 3.1. Dorsal rays before anus 69; total dorsal rays 230; total anal rays 164. Lateral line pores before dorsal origin 35; total lateral line pores 105. Vertebral formula 34/57/116. Proportions and counts of holotype and 8 paratypes are presented in Table 2.

Body only moderately elongate (Fig. 1A), slender, rounded in section along most of its length, depth at gill opening 27 (25–36) in TL, head and trunk 1.8 (1.7–1.8) and head 7.5 (7.1–7.9) in TL. Snout pointed, depressed, its tip turned downwards over tip of lower jaw. Jaws elongate, curved, incapable of closing completely, lower jaw little shorter than snout. Mouth cleft reaching to well beyond eye; lower lip with irregular ridges on its inner surface alongside dentary teeth. Anterior nostril subterminal, a short tube, its rim simple; posterior nostril before and below eye, above free edge of upper jaw, a fully exposed, oblique slit with a free flap on its anterior and ventral rim, the anterior portion being much more prominent and the flap tending to form an anteroventral channel leading downwards to upper edge of mouth (Fig. 1C). Eye very small, diameter 31.9 (26.1–38.0) in head. Interorbital moderately broad. Gill opening crescentic, midlateral, relatively large. Pectoral fin a scarcely visible, extremely weak ridge behind gill opening, supported by several minute rays, the bases of which are visible in the base of the ridge and which project slightly from the free edge. Median fins low, anal fin height less than dorsal. Dorsal fin origin about halfway between gill opening and level of anus. Caudal fin short.

Head pores present and obvious (Fig. 1B), in holotype and 2 NMNZ paratypes on each side as follows: SO 1 + 4, IO 4 + 1, POM 6 + 3 (the 2 CAS paratypes have 2 preopercular pores), ST 2. Lateral line pores present, absent along posterior third of tail.

All teeth prominent (Figs. 1C, 2A), sharp, recurved, relatively few, uniserial and widely separated; in the holotype 2 large and 7 smaller on vomer; 8–9 on maxilla and dentary of which front 2–3 are larger than remainder; 2 or 3 on intermaxillary.

Body colour in isopropyl alcohol light greyish tan, lighter below, with very scattered minute freckles on dorsum of head and snout. Life colour unknown.

Gill arches not well developed; basibranchials absent, hypobranchials 1–2 ossified, hypobranchial 3 absent, ceratobranchials 1–4 ossified, ceratobranchial 5 absent; upper pharyngeal tooth plates closely sutured but not fused, with 17–18 conical teeth; lower pharyngeal tooth plate slender, smaller than upper plates, with 14–15 conical teeth.

Distribution and biology. India, Straits of Malacca, Philippines, Indonesia and northern Australia. Holotype—a female with 0.4 mm ova; all paratypes from Ernakulam (India) are females, except one possible male. The Ernakulam inlet is a large, shallow, turbid estuary; the other localities are apparently much the same, except that the Manila Bay specimen was collected in deeper water.

Etymology. From Greek *zabros* (gluttonous), in reference to the ability of this eel to ingest very large prey (as evident from radiographs of two paratypes [NMNZ 35153, 280 mm TL; MNHN 1998-681, 296 mm TL] that have enormous fish specimens filling out much of the gut cavity). The specimens were caught by fine-mesh

Table 2. Proportions (in thousandths) and counts of the holotype and eight paratypes of *Skythrenchelys zabra* n.sp. Abbreviations: TL = total length, HL = head length, DFO = dorsal fin origin, GO = gill opening, IO = interorbital space; number of specimens in parentheses.

	holotype	mean	range
total length, mm	239	—	119–296
head/TL	133	132.4	127–137
trunk/TL	421	423.6	406–468
tail/TL	446	444.0	405–457
depth at GO/TL	37	34.3	28–40
depth at anus/TL	35	26.7	24–30
DFO/TL	336	332.5	314–356
GO length/HL	122	99.4	81–134
GO interspace/HL	141	135.7	100–162
snout/HL	129	119.8	107–149
upper jaw/HL	282	298.1	252–379
eye/HL	31	30.5	26–38
IO/HL	97	86.8	74–110
dorsal-fin rays			
before anus	69	72.4	64–80
total rays (6)	230	233.3	217–250
anal-fin rays	164	150.1	127–165
lateral-line pores			
before DFO (7)	35	33.9	32–36
before anus (7)	58	56.4	55–57
total pores	105	92.8	90–99
vertebrae			
predorsal	34	33.4	31–36
preanal	57	56.7	55–58
potal	116	118.6	112–122

set net (NMNZ 35153) and by bottom trawl (MNHN 1998-681). That the prey might have been scavenged by the eels from the contents of the nets has to be considered, though the possibility is remote.

Skythrenchelys lentiginosa n.sp.

Figs. 1D–F, 2B

Material examined. HOLOTYPE: female, TL 165 mm, Red Sea, Port Sudan Harbour, 19°38'N 37°07'E, 25 m, rotenone, R. Lubbock and P. Etherington-Smith, 30 July 1972, BPBM 29320.

Diagnosis. A moderately elongate species of *Skythrenchelys* n.gen. with the following characters: tail 51% of TL; dorsal fin arising above anus; pores SO 1 + 4, IO 4 + 1, POM 6 + 1 or 2, ST 2; teeth conical, well-developed, uniserial in jaws and biserial in anterior vomer region; anterior head region and inside of mouth overlain with numerous brown freckles. Vertebral formula 51/50/120.

Further description. Measurements of holotype in mm. Total length 165; head length 20.3; trunk length 60.7; tail length 84; body depth at gill opening 4.6; body width at gill opening 4.2; body depth at anus 3.8; body width at anus 3.5; origin of dorsal fin 84; gill opening length »1.9; gill opening interspace »3.4; snout length 2.5; upper jaw length 7.4; eye diameter 0.8; interorbital space 1.65. Total dorsal rays 208; total anal rays 187. Lateral line pores before anus 50.

Body only moderately elongate (Fig. 1D), robust and nearly round in trunk and anterior tail region, tapering and laterally compressed posteriorly; depth at gill openings 36 in TL; head and trunk 2.0 and head 8.1 in TL. Snout acute, slightly bulbous at tip, without a median groove on its underside. Jaws elongate, curved, incapable of closing completely; centre of eye in anterior 1/3 of upper jaw; lower jaw included, its tip in advance of anterior nostrils. Anterior nostril subterminal, a short tube, its rim simple; posterior nostril entirely outside upper lip, beginning before anterior margin of eye, appearing externally as a large pore with a

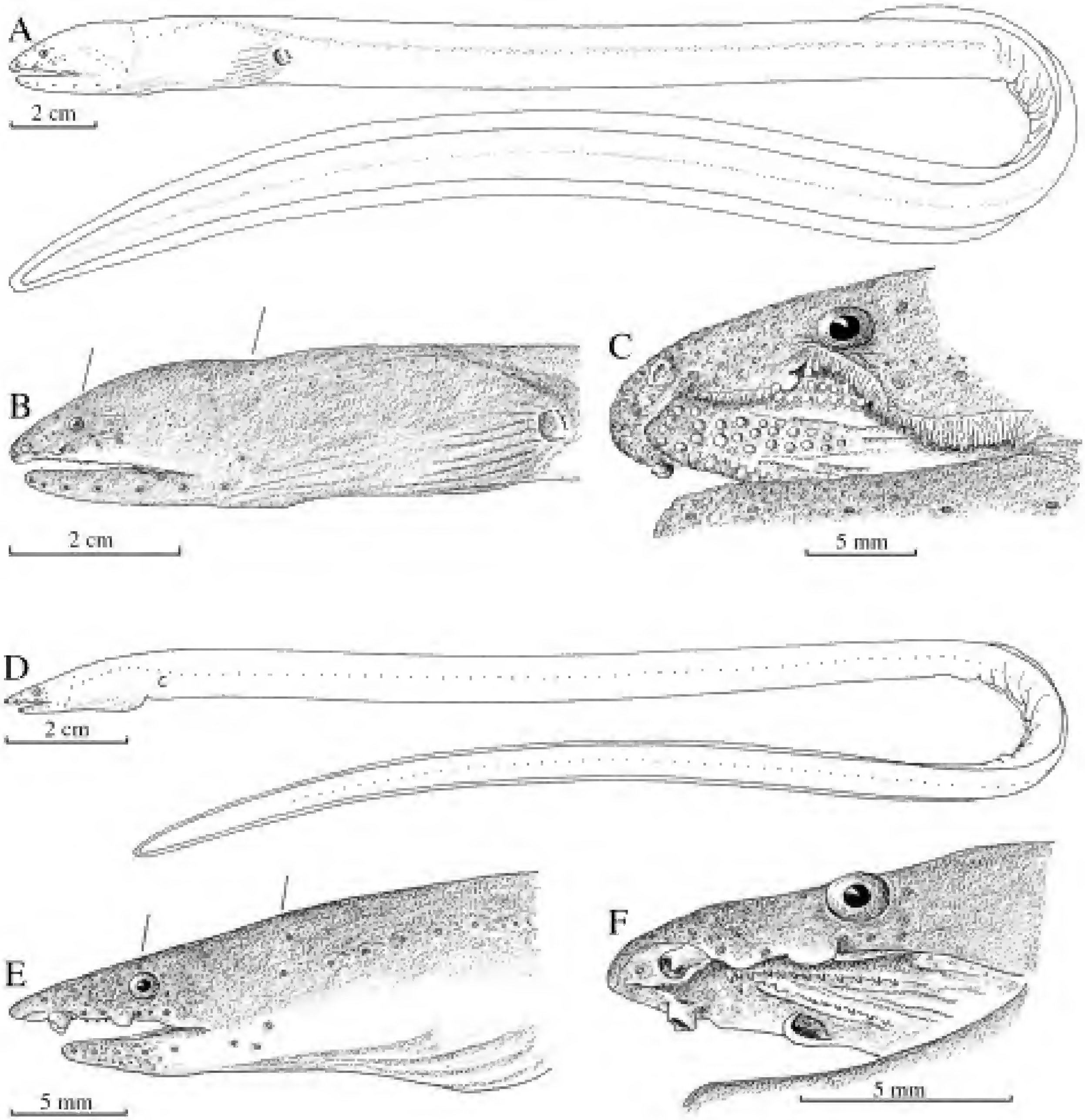


Figure 3. A–C, *Muraenichthys gymnopterus*, BPBM 32816, TL 497 mm; A, body, lateral view; B, head, median pores indicated; C, anterior part of hefad, ventrolateral to show vomerine and maxillary teeth (upper lip turned back). D–F, *Scolecenchelys australis*, NMNZ P.13230, TL 341 mm; D, body, lateral view; E, head, median pores indicated; F, anterior part of head, ventrolateral to show vomerine and maxillary teeth.

small, anterior flap. Eye small, diameter 25.3 in head and about twice in interorbital distance. Interorbital region dome-shaped. Pectoral fins absent. Median fins low, confluent with caudal. Dorsal fin origin above level of anus. Caudal fin very short.

Head pores mostly large and obvious (Fig. 1E), but those of preoperculomandibular series difficult to ascertain and subject to confirmation with the collection of larger specimens; SO 1 + 4, IO 4 + 1, POM 5 + 1 or 2, ST 2. A single pore between anterior and posterior nostrils. Four pores along mandible, 1 or 2 overlying preopercle. Lateral line pores not apparent along posterior third of tail region; approximately 10 pores above branchial basket.

Teeth conical, recurved, and large compared to most myrophines (Figs. 1F, 2B). An anterior intermaxillary block of 5 small teeth, followed by 3 large teeth and a smaller pair of teeth, followed by a uniserial but nonlinear row of 9 vomerine teeth decreasing in size. Maxillary teeth uniserial, 17–18 in a row, decreasing in size. Mandibular teeth uniserial, about 5 smaller teeth near symphysis, followed by 15–16 larger teeth decreasing in size.

Body colour in isopropyl alcohol uniform tan; snout, jaws chin, lips and inside of mouth with many brown to black freckles; numerous fine brown punctations occur above lateral midline; median fins pale; eyes dark blue. Life colour unknown.

Distribution and biology. Known only from the holotype, from the Red Sea. The holotype is a small female with developing ova of 0.3–0.4 mm in diameter; most ophichthids of this size are sexually immature.

Etymology. From Latin *lentiginosus* (freckled), in reference to the speckled head coloration.

Affinities of the two species. After discovering this remarkable specimen in the BPBM collection, McCosker was reluctant to describe it as a new genus and species until larger specimens were discovered. With the collection of many and larger specimens of its congener, *S. zabra* n.sp., we now feel confident in proceeding with its description. The two new species of *Skythrenchelys* n.gen. are easily separable externally on the basis of the origin of their dorsal fin, eye size and dentition (*S. zabra* n.sp. having the dorsal origin further forwards, a much smaller eye and relatively larger teeth), and minor differences in body/tail proportions and dentition. *Skythrenchelys zabra* n.sp. has distinctively large teeth and *S. lentiginosa* n.sp. would not be mistaken for any other ophichthid on the basis of its extraordinary jaw elongation, dentition, and facial coloration.

It is unknown if the coloration of *S. lentiginosa* n.sp. is maintained as it grows, though some facial spotting is likely to remain or even be enhanced with growth. Its facial coloration, eye position, jaw size and developed dentition would suggest a hole-dwelling habitus with only its snout and eyes exposed as is also likely for *S. zabra* n.sp. Such an appearance and lie-in-wait behaviour is typical of species of ophichthine genera such as *Brachysomophis* Kaup, 1856 and *Echiophis* Kaup, 1856 (McCosker *et al.*, 1989).

On the status of *Muraenichthys* and *Scolecenchelys*

As stated in our introduction, several authors (Schultz & Woods, 1949; Gosline, 1951; McCosker, 1970, 1977) have recognised the polyphyletic nature of the many species assigned to *Muraenichthys* but were disinclined to identify the species groups as belonging to separate genera. We have seen most of the type specimens and are confident of the adequacy of most recent descriptions to thereby allow us to divide *Muraenichthys* into two separate phyletic groups. They are separable on the basis of characters described in the key and in Table 1. Specimens of the type species of *Muraenichthys* and *Scolecenchelys* are illustrated in Fig. 3. Aspects of the osteology of *Muraenichthys gymnopterus, Scolecenchelys chilensis, S. gymnotus* and *S. macropterus* are described and illustrated in McCosker (1977).

We provisionally list below the species that we consider to comprise the two genera; the species and their authors are listed in Eschmeyer (1998).

Muraenichthys (type species *Muraena gymnopterus* Bleeker, 1853) includes the following: *Muraena gymnopterus* (and its synonyms *Muraenichthys hattae* Jordan & Snyder, 1901 and *Muraenichthys microstomus* Bleeker, 1865); *Muraenichthys macrostomus* Bleeker, 1865; *Muraenichthys schultzei* Bleeker, 1857; *Muraenichthys sibogae* Weber & de Beaufort, 1916; and *Muraenichthys thompsoni* Jordan & Richardson, 1908 (and its probable synonyms *Muraenichthys malabonensis* Herre, 1923, the type apparently destroyed, and *Muraenichthys philippinensis* Schultz & Woods, 1949).

Scolecenchelys (type species *Muraenichthys australis* Macleay, 1881, by original designation), and its synonyms *Myropterura* Ogilby, 1897 (type species *M. laticaudata* Ogilby, 1897, by original designation) and *Aotea* Phillipps, 1926 (type species *A. acus* Phillipps, 1926, by monotypy) includes the following: *Muraenichthys acutirostris* Weber & de Beaufort, 1916; *Muraenichthys australis* Macleay, 1881 (and probable synonyms *Muraenichthys iredalei* Whitley, 1927, *Muraenichthys lengomena* Scott, 1980, *Muraenichthys lingowenah* Scott, 1975, and *Muraenichthys oliveri* Waite, 1910); *Muraenichthys borealis* Machida & Shiogaki, 1990; *Muraenichthys breviceps* Günther, 1876 (and synonyms *Aotea acus* Phillipps, 1926, *Muraenichthys devisi* Fowler, 1907, and *Muraenichthys ogilbyi* Fowler, 1907); *Muraenichthys chilensis* McCosker, 1970; *Muraenichthys cookei* Fowler, 1928; *Muraenichthys erythraeensis* Bauchot & Maugé, 1980; *Muraenichthys godeffroyi* Regan, 1909 (and probable synonym *Muraenichthys elerae* Fowler, 1934); *Muraenichthys gymnotus* Bleeker, 1857 (and synonyms *Muraenichthys aoki* Jordan & Snyder, 1901, *Muraenichthys fowleri* Schultz, 1943, and *Sphagebranchus huysmani* Weber, 1913); *Muraenichthys japonicus* Machida & Ohta, 1993; *Myropterura laticaudata* Ogilby, 1897; *Muraenichthys macropterus* Bleeker, 1857 (and synonyms *Muraenichthys owstoni* Jordan & Snyder, 1901 and *Echidna uniformis* Seale, 1901); *Muraenichthys nicholsae* Waite, 1904; *Muraenichthys okamurai* Machida & Ohta, 1996; *Muraenichthys profundorum* McCosker & Parin, 1995;

Muraenichthys puhioilo McCosker, 1979; *Muraenichthys tasmaniensis* McCulloch, 1911 (and synonym *M. tasmaniensis smithi* Whitley, 1944); *Chilorhinus (Muraenichthys) vermiformis* Peters, 1866; and *Muraenichthys xorae* Smith, 1958. *Incertae sedis*: *Muraenichthys moorii* Günther, 1870. Note that adjectival suffixes of species transferred from *Muraenichthys* to *Scolecenchelys* will change, in that *enchelys* is feminine.

ACKNOWLEDGMENTS. Many individuals have generously assisted with this study, and we thank the following: D. Catania, M. Huong and J. Fong (CAS); J. Llewellyn, Victoria University of Wellington, New Zealand, for the preparation of radiographs and other assistance; R. Drewes (CAS) for staining and clearing specimens; E. Böhlke, Academy of Natural Sciences of Philadelphia, for her advice and the use of her vertebral data. Many curators and collection managers have allowed us to examine specimens in their care, including: E. Böhlke (ANSP); J. Paxton, D. Hoese and M. McGrouther (AMS); A. Woolger and O. Crimmin, Natural History Museum, London; J. Randall and A. Suzumoto (BPBM); W. Eschmeyer and T. Iwamoto (CAS); A. Graham (CSIRO, Hobart); M. Bauchot, G. Duhamel and P. Bearez (MNHN); M. Gomon, Museum of Victoria, Melbourne; R. Rosenblatt (SIO); and the staff of the U.S. National Museum (USNM). We thank Carl Ferraris for reading a draft of this manuscript. Much of this project was accomplished during McCosker's tenure as a Visiting Fellow at the Australian Museum, Sydney; research assistance to Castle was funded by the Internal Grants Committee (VUW) and leave funds from the Leave Committee (VUW).

References

Böhlke, E.B., 1982. Vertebral formulae of type specimens of eels (Pisces: Anguilliformes). *Proceedings of the Academy of Natural Sciences of Philadelphia* 134: 31–49.

Böhlke, E.B., 1989. Methods and Terminology. In *Fishes of the western North Atlantic, Vol. I. Orders Anguilliformes and Saccopharyngiformes*, ed. E.B. Böhlke, pp. 1–7. *Memoirs of the Sears Foundation for Marine Research* 1(9): 1–655.

Dingerkus, G., & L.D. Uhler, 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* 52: 229–232.

Eschmeyer, W.N., ed., 1998. *Catalog of Fishes*. Special Publication No. 1 of the Center of Biodiversity Research and Information, California Academy of Sciences, 3 vols., pp. 2905.

Gosline, W.A., 1951. The osteology and classification of the ophichthid eels of the Hawaiian Islands. *Pacific Science* 5: 298–320.

Kaup, J.J., 1856. Uebersicht der Aale. *Archiv für Naturgeschichte* 22(1): 41–77.

Leiby, M.M., 1989. Family Ophichthidae: Leptocephali. In *Fishes of the western North Atlantic, Vol. II. Orders Anguilliformes, Saccopharyngiformes, Notacanthiformes, Elopiformes*, ed. E.B. Böhlke, pp. 764–897. *Memoirs of the Sears Foundation for Marine Research* 1(9): 657–1055.

Leviton, A.E., R.H. Gibbs Jr., E. Heal & C.E. Dawson, 1985. Standards in herpetology and ichthyology: part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985: 802–832.

Lütken, C.F., 1851. Nogle bemaerkinger om naeseborenes stilling hos de i gruppe med *Ophisurus* staaende slaegter af aalefamilien. *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjöbenhavn*, 1851 (1/2): 1–21.

McCosker, J.E., 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the description of a new genus, *Schismorhynchus*, and a new species, *Muraenichthys chilensis*. *Pacific Science* 24: 506–516.

McCosker, J.E., 1977. The osteology, classification, and relationships of the eel family Ophichthidae. *Proceedings of the California Academy of Sciences* 41(1): 1–123.

McCosker, J.E., E.B. Böhlke & J.E. Böhlke, 1989. Family Ophichthidae. In *Fishes of the western North Atlantic, Vol. I. Orders Anguilliformes and Saccopharyngiformes*, ed. E.B. Böhlke, pp. 254–412. *Memoirs of the Sears Foundation for Marine Research* 1(9): 1–655.

Schultz, L.P., & L.P. Woods, 1949. Keys to the genera of echelid eels and the species of *Muraenichthys* of the Pacific, with two new species. *Journal of the Washington Academy of Sciences* 39: 169–174.

Wade, C.B., 1946. Two new genera and five new species of apodal fishes from the eastern Pacific. *Allan Hancock Pacific Expeditions* 9(7): 181–213.

Manuscript received 11 September 1998, revised 21 December 1998 and accepted 11 January 1999.

Associate Editor: J.M. Leis.

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 123–140. ISSN 0067-1975

A New Species of the Devonian Lungfish *Dipnorhynchus* from Wee Jasper, New South Wales

K.S.W. CAMPBELL AND R.E. BARWICK

Department of Geology, Australian National University, Canberra ACT 0200, Australia
ken.campbell@anu.edu.au
richard.barwick@anu.edu.au

ABSTRACT. A new large mandible of *Dipnorhynchus* from the Early Devonian *serotinus* Zone (late Emsian) at Wee Jasper, is given the status of a new species, *D. cathlesae* n.sp. This fossil characterised by its size; relative depth with respect to its length; short anterior furrow, deeply bordered by a raised broad rim of dentary between itself and the labial pit; large foramen for a nerve in the posteromedial end of the labial furrow; a strong furrow from the adductor pit to the posterior end of the labial pit; thick dentary; lack of tubercles (blisters) on the prearticular plate; and an adductor pit wide posteriorly and narrowing gradually anteriorly. The surface of the tooth plate is not made of dentine, but of bone formed on the surface of the prearticular. This species represents the youngest known occurrence of *Dipnorhynchus* in the Murrumbidgee sequence.

CAMPBELL, K.S.W., & R.E. BARWICK, 1999. A new species of the Devonian lungfish *Dipnorhynchus* from Wee Jasper, New South Wales. *Records of the Australian Museum* 51(2): 123–140.

Early Devonian dipnoans were beginning a period of rapid evolution. The number of species is limited at present, but many of them are beautifully preserved in limestone, and can be extracted as three dimensional fossils with acetic acid. The specimens from Wee Jasper on the Burrinjuck Dam, New South Wales, are among those that have produced the best information on undistorted material. *Dipnorhynchus* is the most abundant of these genera. Herein we describe a new species of *Dipnorhynchus, D. cathlesae.*

The limestone-shale sequence at Wee Jasper and Taemas covers a range from the *dehiscens* Zone to the *serotinus* Zone of the Emsian. The rocks are more or less continuously fossiliferous and include many marine invertebrate fossils including corals and brachiopods. Remains of the dipnoan *Dipnorhynchus* have been previously described from several levels at both Taemas and Wee Jasper, but a recent discovery of a mandible of this genus towards the top of the sequence provides information on its subsequent evolution. The specimen was discovered by Ian and Helen Cathles of Cookmundoon Station, Wee Jasper.

Most of the rocks were deposited in shallow subtidal environments, but occasional supratidal deposits are also found. All the specimens of *Dipnorhynchus* were found in the subtidal limestones.

The specimen herein described shows large neural openings into a labial pit, the outer edge is formed by a high margin of the surangular; reduced dental structure (tubercles) on the prearticular; and the great height of the

Table 1. Comparison between the dimensions of the holotype of *Dipnorhynchus cathlesae* and the largest known specimen of *Dipnorhynchus kurikae* Campbell & Barwick (ANU 60030).

species	width at mandibular articulation (cm)	length (cm)	maximum depth of mandible (cm)	maximum depth of dentary (cm)
D. cathlesae	22	19	10	6.5
D. kurikae	15	14	5.5	3

posterior face of the mandible leaving a shallow space for the tongue mass. We interpret these features to mean that the suction capacity of the animal was increased beyond what is shown by the earlier species, that the tooth plates were modified to be crushers of food, and that the capacity of the hyoid apparatus to move forward and backwards was greatly reduced.

This specimen is so large that when it was first observed in the rock, it was not recognised as a dipnoan. The major dimensions are outlined above (Table 1), and are set against the largest known specimen of *D. kurikae* (Campbell & Barwick, 1985). Note that *D. kurikae* is dwarfed by the specimen of *D. cathlesae*, especially in its depth.

The specimen was exposed on the rock surface and its posterior face was weathered. It was collected in five fragments, four of which were in association and one was isolated. The associated fragments were separated by cracks and breaks in the rock, and they fell apart on collection. Reassembly showed that fragments of bone were missing from some of the edges, but by and large the fragments could be restored sufficiently to permit us to make a description of most of the osteological features. The isolated

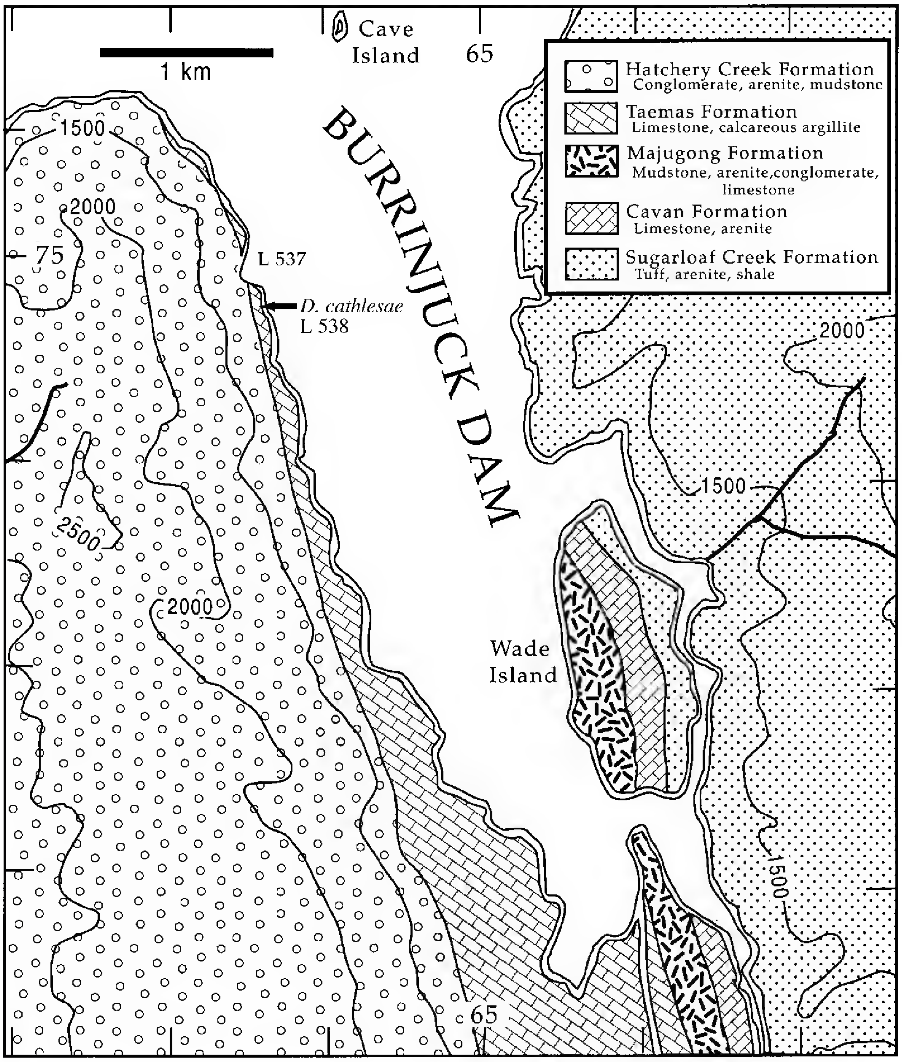


Figure 1. Map of the northern part of the Wee Jasper outcrop of the Lower Devonian Limestones, modified after Pedder *et al.* (1970). The numbers L 537 and L 538 refer to the collection data of Pedder *et al.*

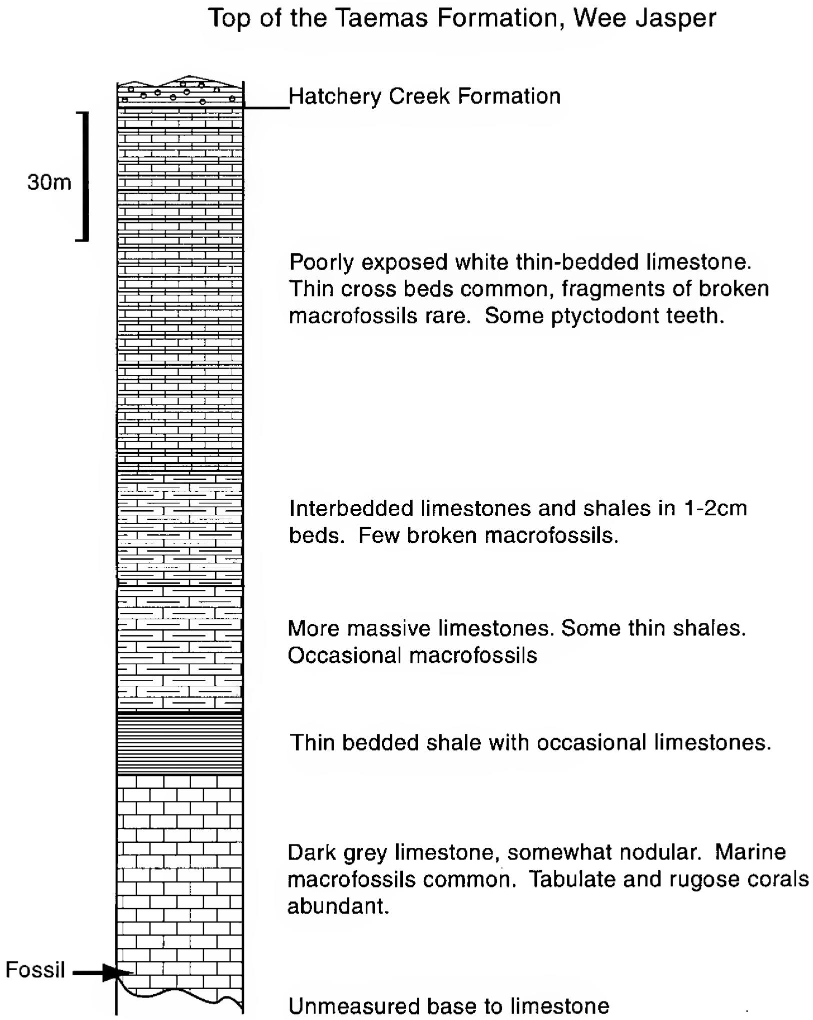

Top of the Taemas Formation, Wee Jasper
Hatchery Creek Formation
30m
Poorly exposed white thin-bedded limestone. Thin cross beds common, fragments of broken macrofossils rare. Some ptyctodont teeth.
Interbedded limestones and shales in 1-2cm beds. Few broken macrofossils.
More massive limestones. Some thin shales. Occasional macrofossils
Thin bedded shale with occasional limestones.
Dark grey limestone, somewhat nodular. Marine macrofossils common. Tabulate and rugose corals abundant.
Fossil
Unmeasured base to limestone

Figure 2. Stratigraphic section measured from the locality where *Dipnorhynchus cathlesae* was collected up to the Hatchery Creek Formation.

fragment was found down slope from the original specimen, and consists of a piece of a mandible that fits a section missing from the original. No other bone fragments are found in the vicinity and the bone size in the fragment matches the main specimen.

In the absence of other bones in the sediments around the point where the specimen was recovered, and despite several detailed searches in the surroundings, which are well exposed because the withdrawal of the waters of the Burrinjuck Dam in the 1998 drought, we conclude that any other specimens of the species that lived in the area have not been preserved in observable rocks. In the sediments overlying the specimen there are several layers of limestone containing ptyctodont fragments, but these rocks have not yielded any large fragments of bone.

Stratigraphy

A map showing where the specimen was collected is given in Fig. 1, and the stratigraphic sequence of the upper part of the Taemas limestone at Wee Jasper is presented in Fig. 2.

The uppermost unit below the Hatchery Creek Formation consists of very thin bedded white limestones, many beds being only 1 mm thick. The unit is c. 69 m thick. Some crossbedding is present. The rocks are interpreted as an intertidal zone carbonate deposit, which is consistent with the fact that the overlying unit is the fresh water Hatchery Creek Formation. The limestone has few invertebrate macrofossils, but ptyctodont tooth plates are occasionally present.

Immediately beneath this unit are three strata consisting of interbedded limestones and shales. These contain few macrofossils, but occasionally they have a few ptyctodonts. Together these three units are c. 58 m thick.

Our specimen comes from c. 40 m below the top of the limestone beneath the above mentioned three units, near the locality listed as by Pedder *et al.* (1970) as L538 at the northern end of the Taemas limestone outcrop. This lower limestone is different in kind from those lying above it, being a dark grey colour, often nodular, and in units some centimetres thick. It was deposited in an environment which supported a rich marine life. The commonest fossils are the thamnoporoid and favositid tabulates associated with an abundant ceroid syringoporoid probably related to *Romeripora* (Hill & Jell, 1970). The corals are all rolled and show a variety of shapes, indicating that at least during the final depositional event, a rough water environment existed. The rugosans have been described by Pedder in Pedder *et al.* (1970), and fig. 4 of that paper lists seven species of corals which are restricted to this level. Garratt & Wright (1989) have indicated that this unit belongs to their Coral Zone F. The conodonts were also described by Philip & Jackson in Pedder *et al.* (1970), and subsequent work outlined by Basden *et al.* (1999) indicates that they belong to the *serotinus* Zone of late Emsian age. Other fossils in the dipnoan bearing limestone include stromatoporoids and gastropods. Brachiopods are rare. The fossil site is c. 142 m beneath the Hatchery Creek Formation.

One peculiarity of the occurrence is the fact that no other bone was found anywhere in the vicinity. In the Wee Jasper sequence, fragments of placoderms are commonly found near dipnoans, but prolonged searches at this locality failed to find bone of any kind.

The locality is on the flank of the syncline of which the axis lies nearby. Hence the rocks have been subject to the cleavage which is common in the area, and the dipnoan specimen is somewhat distorted. Despite this the specimen restoration is not badly deformed.

Systematic palaeontology

Genus *Dipnorhynchus* Jaekel, 1927

Type species. *Ganorhynchus sussmilchi* Etheridge Jr., from the *Spinella yassensis* Limestone at Taemas, Burrinjuck Dam, New South Wales.

Remarks. Although we have no skull of the new species described herein, we confidently assign the mandible to *Dipnorhynchus*. It displays the main features of the mandible of that genus, and it has no evidence of teeth on the prearticulars which should be there if it were related to *Speonesydrion*, the only other genus of dipnoans found in this stratigraphic sequence.

The specimen was prepared by etching with acetic acid, so that much of the internal structure which is not visible on other more complete dipnorhynchids, was directly observable on this specimen. To hold some of the more fragile parts in position, thin wooden struts were placed in position, and these can be seen on Fig. 3.

Dipnorhynchus cathlesae n.sp.

Holotype. ANU60027, from the upper part of the Taemas limestone, near L538 on the map of Pedder *et al.* (1970). Specimen on loan from I. & H. Cathles, Cookmundoon Station, Wee Jasper.

Diagnosis. Large species with its height relative to length greater than in any other members of the genus; dentary with a high lateral edge; labial pit deep and bordered by a high margin composed of the surangular; large neural connection from the adductor cavity to the labial pit; a large groove extends from the adductor pit to the labial pit; lingual space very shallow; no tubercles (blisters) on the prearticular tooth plate.

Remarks. Our first reaction was that the specimen was a large adult of *D. kurikae*, a species found in the *Receptaculites* and at the top of the Bloomfield Limestone, lower down in the stratigraphic sequence. The largest specimen of that species we have collected is a palate described by Campbell & Barwick (1985: fig. 5), but it is smaller than the present specimen. A number of characters found in this new specimen are of the same kind as those found in other dipnorhynchid species, but their proportions differ. On the other hand, some features are different in kind from what are known elsewhere. For these reasons we have decided to describe the specimen as a new species. We now refer to the individual characters separately.

1. In comparison with other dipnorhynchids, the **labial pit** (Figs. 5, 6B–D, 10) is a short deep structure. Its lateral edge, formed from the surangular, is high and makes a distinct margin, turned inwards along its dorsal edge and slightly overhangs the pit. Posteriorly, this edge rises up to join the edge of the surangular forming the outer edge of the adductor fossa, leaving a groove (a labial groove, Figs. 4A, 10) along the inner face of that bone. This labial groove, which is up to 6 mm in diameter, runs from the anterior margin of the adductor fossa into the lowermost margin of the labial pit. It can be traced along the inner face of the dermal bones for about 2 cm posterior to the anterior end of the adductor fossa, gradually becoming less clear posteriorly. The inturned edge of the dermal bone which overhangs it is covered by fine granules as are common along the more posterior edge of the surangular. The breadth of this granulated area is narrower than is found in specimens of *D. kurikae*.

In its depth and continuity into the adductor chamber this groove is unlike any structure which we have observed in other dipnorhynchids. In *D. kurikae*, the labial pit is shallow and does not have an upturned lateral margin. In *D. sussmilchi* the labial pit is even shallower, and its lateral margins are downturned rather than forming a rim. In *D. kurikae* a slight groove is present running along the floor of the labial pit and, running along the flattened surface of the bone behind the labial pit, it enters the adductor fossa at its *anteromedial* end. This is the boundary between the surangular and the bone forming the remainder of the floor of the labial pit. Clearly this cannot make any impression on the inner face of the surangular, and it is not in the same position as the groove in *D. cathlesae*.

Did this groove in *D. cathlesae* house a vessel, or a nerve, or a muscle or a ligament? We do not accept that it was a nerve because of its size, and because the abundant supply of nerves observed elsewhere in the labial pit make the same pattern we have observed in other dipnorhynchids (Thomson & Campbell, 1971: figs. 20, 41, 80; Campbell & Barwick, 1985: figs. 8a, 9a). In particular a large foramen at the *posteromedial* end of the labial pit passes outward from the adductor chamber through bone beneath the posterior end of the dentary. This carried a nerve from the adductor chamber to the labial pit; it also carried a branch which turns forward into the posterior end of the anterior fossa. Because it carries the two branches, the foramen at the posterior end of the labial pit is obviously double internally but apparently single externally. The foramen joins the labial pit and the longitudinal groove by a deep furrow on the right side of the specimen, but on the left the furrow is much shallower, and has a small anteriorly directed furrow opening out of its margin. In extant dipnoans, only nerves V and VII extend forwards to this position. These would have supplied the sensory nerves to the soft tissues in the anterior furrow and the labial pit. Other nerves which enter the labial pit pass into the base of the pit via a large number of foramina (Figs. 6C,D). These open down into the adductor cavity, and they would have carried nerves and vessels which entered the labial pit. Thus we can account for a nerve and blood supply to the lip, and so there is no need for a large nerve or the provision of a blood supply from the adductor chamber through the foramen under discussion.

Therefore this labial groove must have carried a muscle or a ligament from the adductor pit to the lip. The lips of extant lungfish take an active part in the feeding mechanism (Bemis, 1987, for summary). In his comments on the lips and tongue, Bemis noted that chondroid tissue plays an important part in outlining the shape of the lips. In *Lepidosiren*, the upper and lower lips engage each other to make a surface against which the inflow of water can be controlled. *Protopterus* has a different and more complicated system. We have no reason to think that our new primitive form followed either of these patterns, but the presence of large lip spaces suggests that the ability to be a suction feeder was already present in the Devonian. Other dipnorhynchids did not have a large groove running into the labial pit as does *D. cathlesae*, and yet they probably possessed a suction feeding capacity. Hence we conclude that the capacity to produce suction feeding was present without the structure in the groove in question. However, the fact that the lips are known to be of major importance for suction in extant dipnoans, and different means for improving suction were evolved by different extant genera, it seems reasonable to infer that *D. cathlesae* had developed an improved method for suction in comparison with previous members of the genus.

As the groove runs posteriorly into the adductor fossa where it loses contact with the dermal bone and would have been adjacent to the adductor muscles, the soft tissue could have contained an offshoot from the adductor musculature. This is of interest because the lip retractor muscles of *Lepidosiren* and *Protopterus* are derived embryologically from the adductor mass (Bemis, 1987: 262). On the other hand, the groove could have contained chondroid tissue connected into the adductor muscle chamber. The information we have at present does not allow us to choose between these two hypotheses.

2. In all dipnorhynchids, the well-defined **anterior furrow** (Figs. 4A, 7A,B) is completely surrounded by bone in dorsal view. It is bounded anteriorly and laterally by the dentary, and posteriorly by the prearticular. In all the other known species of dipnorhynchids, the anterior furrow is long and narrow. In some specimens it is divided by the prearticular joining the dentary medially, but the distribution of this feature among populations shows that it is subject to intraspecific variation. In *D. cathlesae* the anterior furrow is present and is enclosed in the usual way for a dipnorhynchid, but it is shorter and wider in dorsal view than in other dipnorhynchids. Part of this may be due to the fact that the prearticular extends slightly over its posterior end. Despite this, the furrow is less than two-thirds the length of the dentary.

The anterior end of the furrow is overhung by the dentary which turns down into the furrow, and is bounded by a strong ridge parallel with the anterior edge of the furrow. Medially on this edge there is a narrow thin protrusive layer which has the appearance of dentine. Deeper into the furrow, the dentary forms a groove which is bounded ventrally by a thin line where it joins the endoskeletal bone. On the posterior face of the anterior furrow the dental plate overhangs, leaving a groove. This groove is at about the same level as the groove in the dentary around anterior furrow mentioned above. We conclude that a layer of soft tissue formed within the anterior furrow, protecting the soft (sensory) tissue filling the lower part of the anterior furrow. Presumably this covering layer must have contained many perforations to permit interaction with the sensory tissue beneath. From its position we think that it was a chemosensory structure at the entrance to the mouth.

The floor of the furrow is formed of open textured endoskeletal bone which contains several foramina. These foramina (Figs. 7A,B) are present on both sides of the specimen, though they are differently disposed with respect to the mid-line. This is normal for dipnorhynchids (Campbell & Barwick, 1985). The right side of the specimen has at least six large foramina similarly opening downwards into either the anterior end of the adductor chamber, or the space occupied by tubules between the adductor chambers.

The posterolateral corners of the anterior furrow are strongly overhung by the edge of the prearticular dental plate. High up in the posterolateral corner of the anterior furrow is a foramen which opens via a long tube, which is entirely concealed in bone, into one of the foramina making up the large unit at the posterior end of the labial pit (Fig. 10). The second foramina in this unit also sends a nerve into the posterior end of the labial pit. This nerve would have been either V or VII, as comparison with *Speonesydrion iani* shows (Campbell & Barwick, 1984: fig. 25).

3. The **dentary** (Figs. 4A, 6B–D, 10) is much thicker dorsoventrally than that of any other dipnorhynchid. Ventrally it is not separated from the infradentaries by the slight groove which is common on all other dipnorhynchids, but it grades smoothly into the infradentaries. Along its dorsal surface the median part is smooth, depressed beneath the levels of the lateral parts, and does not support a transverse ridge. Laterally the dentary is also well rounded on its dorsal surface, and the surface continues forward to the level of the anterior end of the anterior furrow. In other dipnorhynchids the lateral surface of the dentary decreases height more posteriorly. In *D. kurikae* at all stages of growth, the dentary has a secondarily thickened ridge along the lateral crest. No sign of such a ridge is present in *D. cathlesae*. Nor is there present a thickened ridge along the anterior margins of the dentary making a distinct feature in *D. kurikae*.

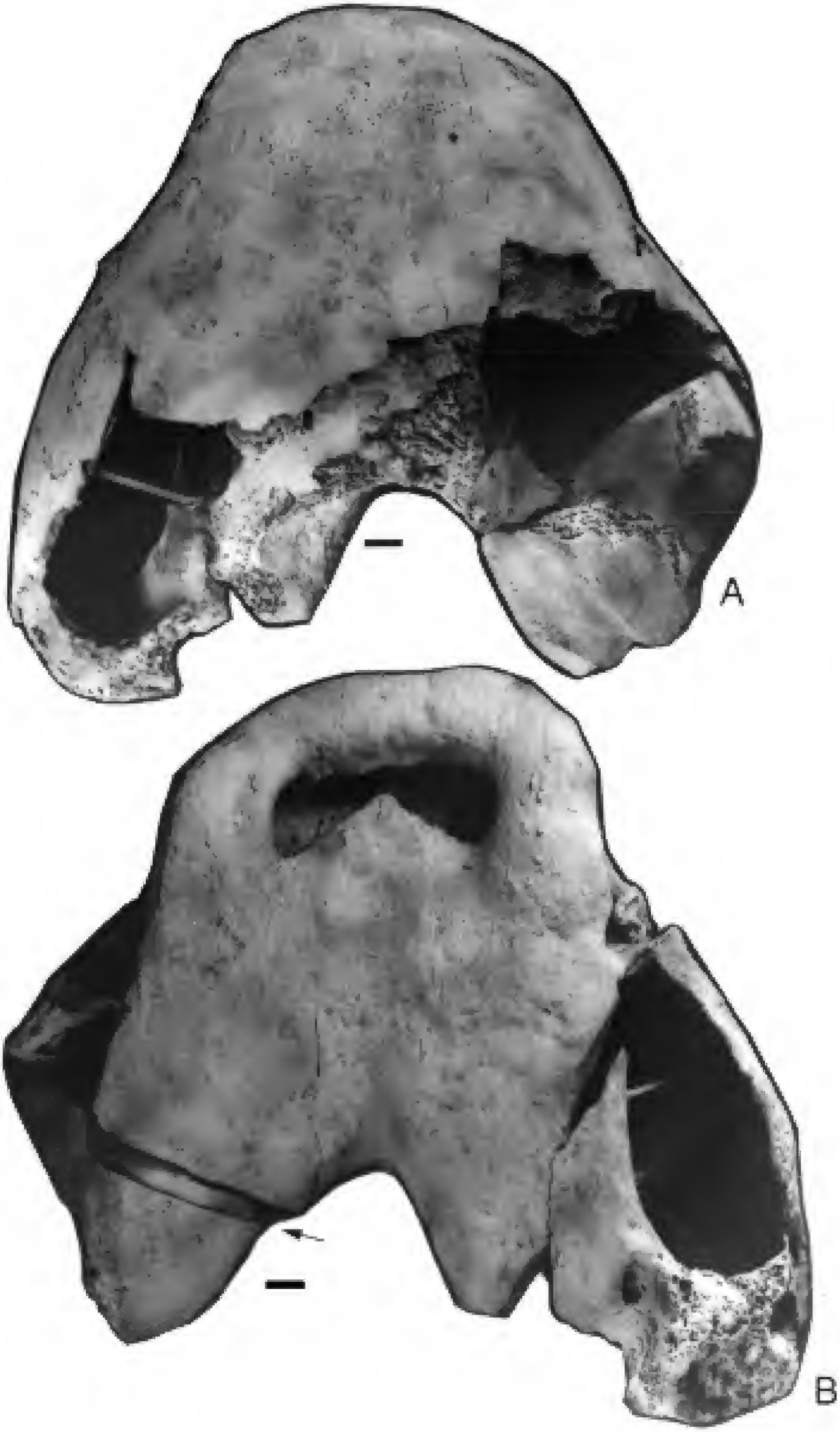


Figure 3. A, ventral and B, dorsal views of the holotype of *Dipnorhynchus cathlesae*. Photographs are greatly reduced in size. Arrow indicates where sections shown on Figs. 11–14 were cut. Isolated left fragment not included in figure, see Fig. 4. Scales = 1 cm.

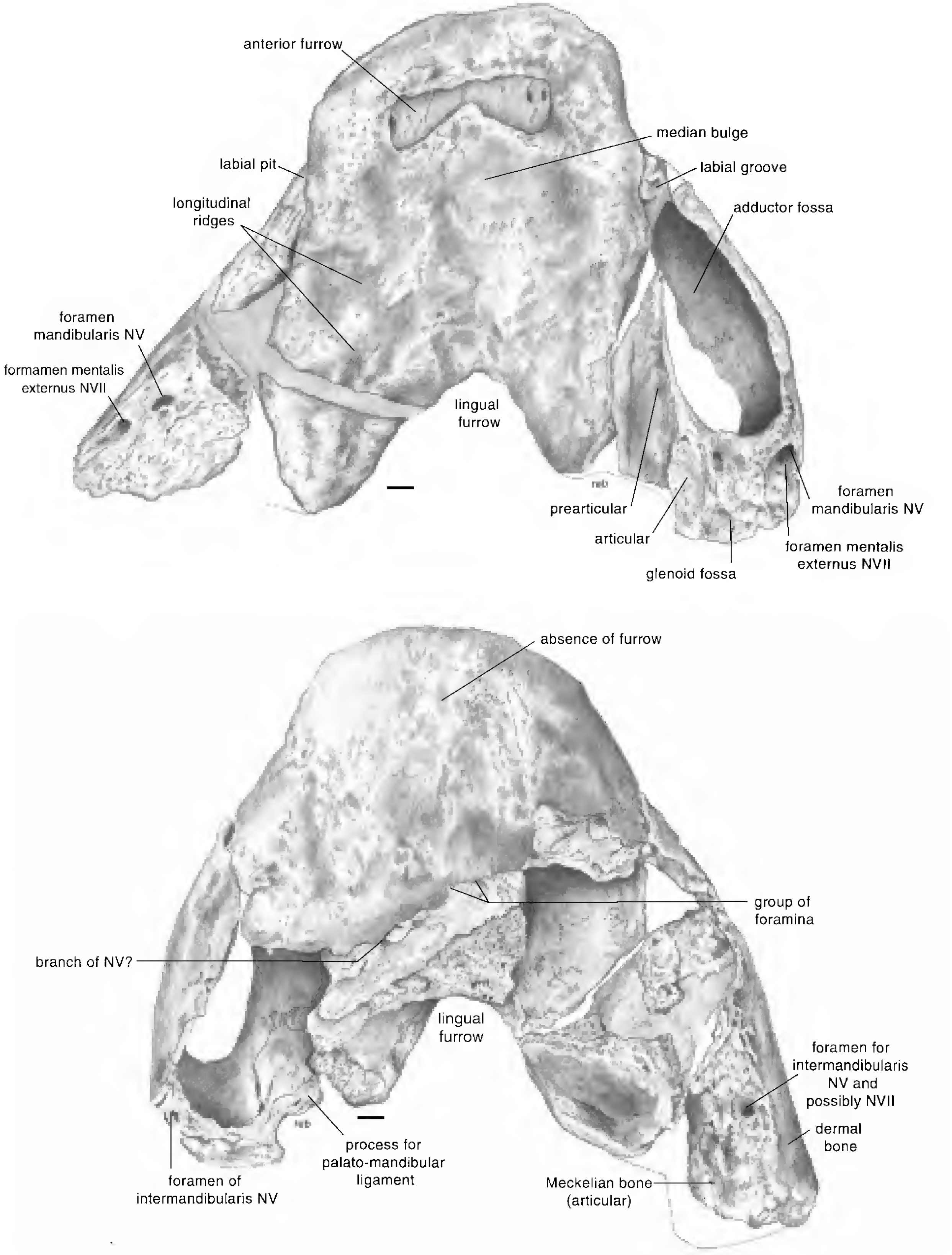


Figure 4. Reconstruction of the mandible of *Dipnorhynchus cathlesae* in dorsal and ventral views. The isolated part in the left side of the specimen did not fit back perfectly, and are shown in two slightly different positions on A and B. Scales = 1 cm.

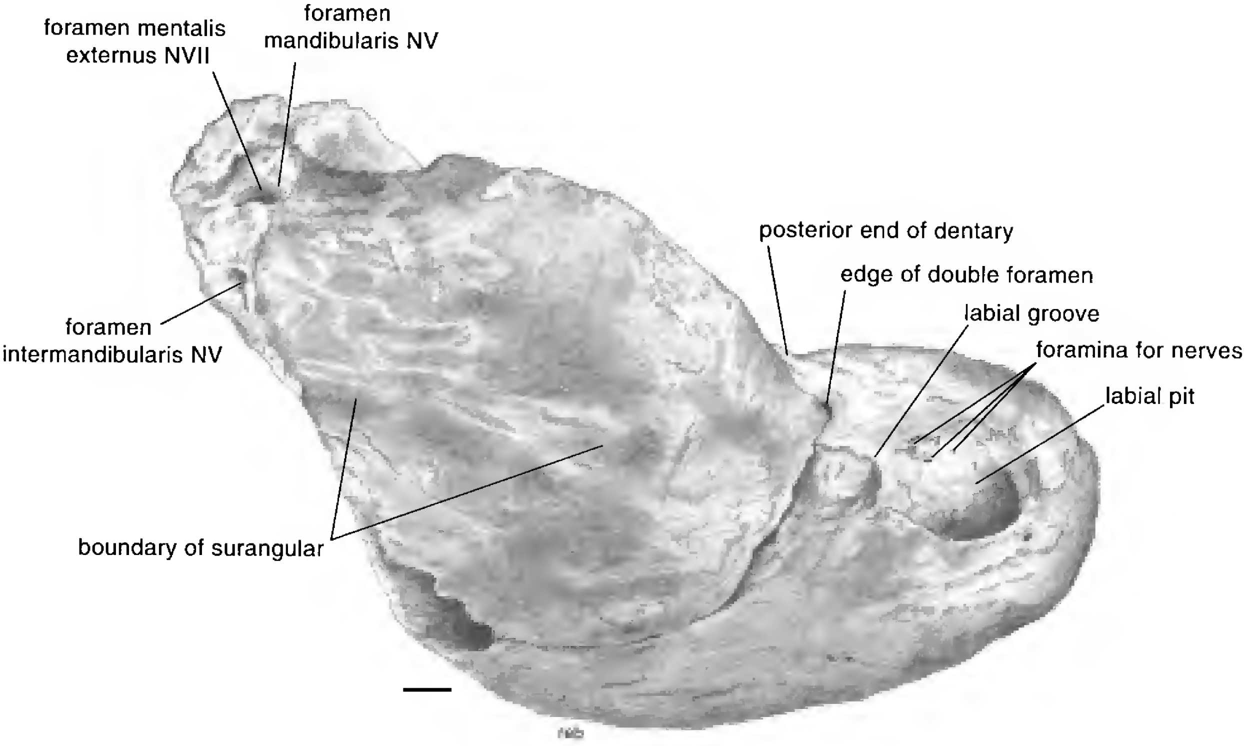


Figure 5. Right lateral view of the mandible of *Dipnorhynchus cathlesae*. The margin of the surangular is not clear and we have marked its ventral edge as "surangular" in its most probable position. Scales = 1 cm.

4. The **dental plate** (Figs. 3B, 4A, 7C) on the prearticular is up to 1.8 cm thick. It does not have any thick tubercles (or blisters; see White, 1966) such as occur in other dipnorhynchids. Surprisingly, this statement includes the large posterior tubercles (or blisters) as well as the anterior tubercles behind the anterior furrow. Is it possible that large tubercles were present originally, but have been removed by wear? Remaining on the surface are two or three low rounded longitudinal ridges, and a flattened median elevation behind the anterior furrow. In another work, we have shown that the eminences on the tooth plates in dipnorhynchids were formed by the addition of new tissue to the surfaces by upgrowth of new tissue on top of the underlying bones (Campbell & Barwick, in press), and in the discussion below, we discuss this matter further. Such eminences were modified by wear, but they were renewed on their surfaces by deposition from bony tubes through the underlying bone. Were the prearticulars smooth because of wear or because they were always without eminences? We have examined 12 mandibles of other dipnorhynchids, and on every one of them there is clear evidence of tubercles (blisters), even if they have been worn. Hence *D. cathlesae* is unique among dipnorhynchids in the structure of this part of its dental plate. Moreover the specimen has a distinct groove in the surface where other species have an anterior tubercle. So far as we are able to determine, this means that the dental surface was approximately flat, rather than tuberculate, throughout growth, and that the species crushed its food on a simple irregular grinding surface.

The margins of the prearticular against the adductor chamber consist of a sharp ridge without any sign of a rounded biting surface. Posteriorly this sharp ridge, formed by the junction of the dentine with the underlying bone, falls steeply into the posterior surface of the prearticular plate. The posterolateral surface adjacent to this dentine edge, makes a concave face medial to the glenoid fossa, and contains a wide open bony furrow which seems to have been floored, at least in part, by the articular laterally and the prearticular ventrally. The anterior part of this furrow has a broad shallow pit in which two or three nutrient openings are found (Fig. 6F). The posterior end of the structure is broken through, and clearly shows the coarse articular bone extending ventrally beneath the prearticular. Other well-preserved dipnorhynchids do not have a furrow in this position. On the contrary, the area is smooth, and passes posteriorly into the ridge on which was attached the pterygoid-mandibular ligament. Only the base of the pterygoid-mandibular ligament remains after breakage in *D. cathlesae*. The furrow described above must have been occupied by thick soft tissue forming the inner face of the glenoid fossa.

Although the glenoid fossa is not well preserved, it is known to be a posterodorsally directed opening, and is confined medially by a low bony ridge (Figs. 3B, 6F). Although the lateral and rotational movement of the mandible must have been controlled by the adductor muscles and a pterygoid-mandibular ligament, we also consider that the thick band of tissue in the position indicated would have served as a stabilising feature, confining the medial boundary of the glenoid fossa. The pressure on the

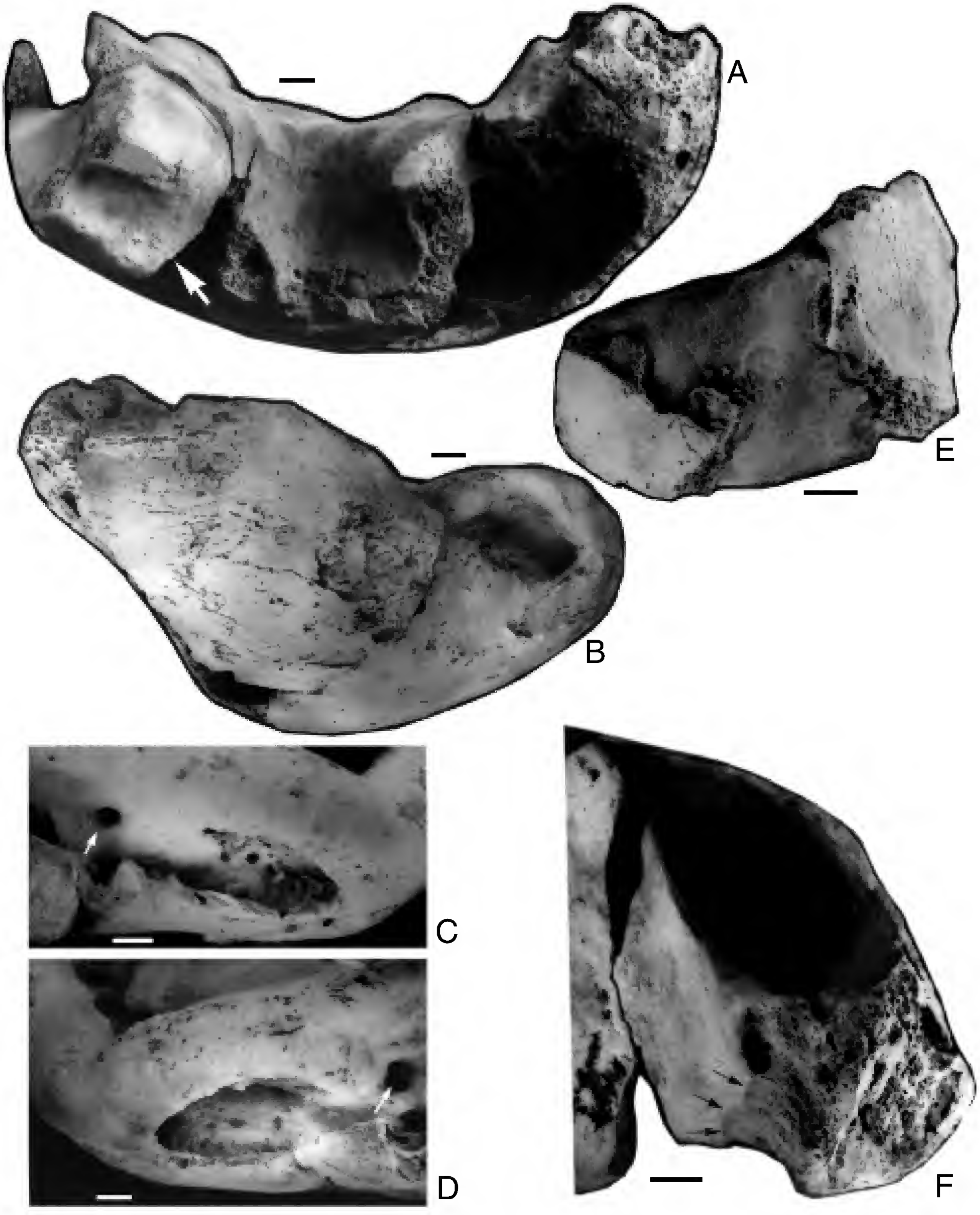


Figure 6. *Dipnorhynchus cathlesae*: A, posterior view; B, lateral view; C, D, dorsolateral views into the right and left labial pits. Note the foramina in the floors of the pits and the large foramina at their posterior ends, indicated by a white arrow in C and D. E, part of the mandible from the left side which was found down slope from the main specimen. Its position is shown by the large white arrow in Fig. 6A. Left side is external dermal bone; right side is the posterior face of the prearticular to the top left of the white arrow in Fig. 6A. Medial surface is where external bone was stripped off during preservation. F, right posterior end of the mandible showing the broken glenoid fossa, the sharp edge on the tooth-plate against the adductor fossa, and the sharp edged groove between the tooth-plate and the glenoid, marked by black arrows. Scales = 1 cm.

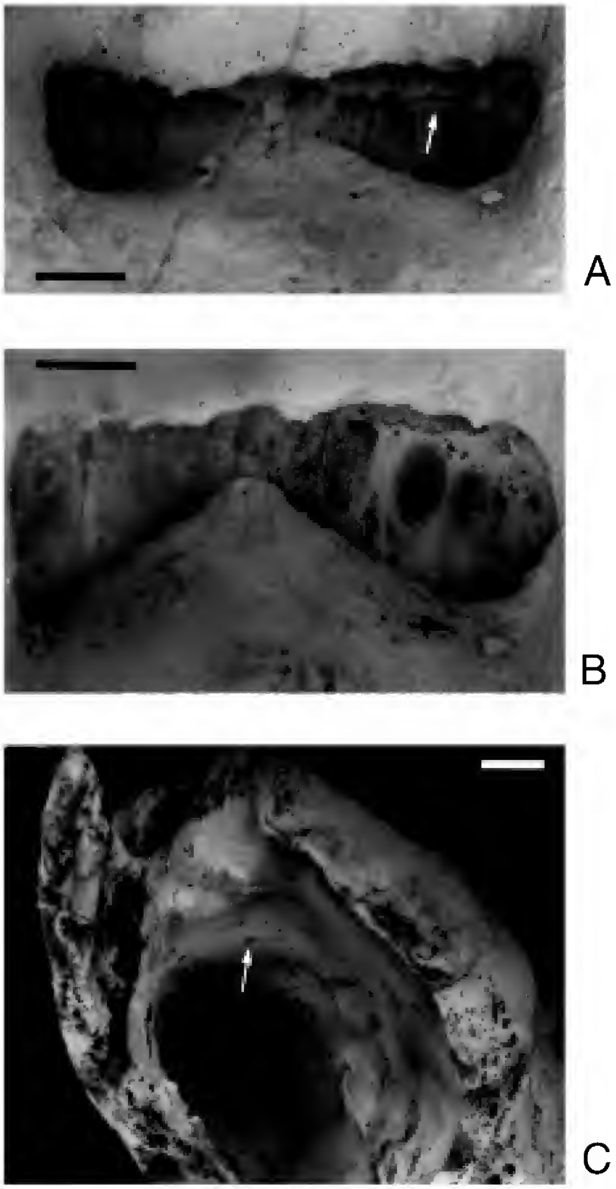


Figure 7. Two views into the anterior furrow of *Dipnorhynchus cathlesae*. A, with the specimen horizontal and B, with it tilted forwards. Note the abundance of pits on the right side and their scarcity on the left. The line of junction between the dentary and the endocranial bone shown by a white arrow. C, view down the adductor chamber on the left side of the specimen. The thickened prearticular is on the right. Note the ridges on the right wall, and the foramen (white arrow) with a short groove leading to the foramen at the posterior end of the labial pit. Many other nutrient foramina are also shown. Scales = 1 cm.

glenoid during a bite must have been very strong, and if large prey were being ground up on the dental plates, one would expect rotational forces to be periodically increased. Under these conditions, it is not surprising that extra support of the glenoid was developed.

The anterior end of the tooth plate is triangular in outline, but it does not rise up towards the dentary. On the contrary it declines perceptibly towards the anterior furrow, leaving behind it a gentle, rather flattened eminence. Against the anterior furrow, the tooth plate strongly overhangs the underlying endoskeletal bone.

We note that in *D. kurikae* the margins of the dental plate show signs of active growth and modification. In particular this applies to a small patch of the plate medial to the glenoid fossa, and along the posterior edge of the plate within and lateral to the lingual furrow. At these localities the continuous layer of dentine has a sharp margin, and patches of rounded or slightly elongate denticles occupy the surface. These indicate that the plate was growing at these points when death occurred. In *D. cathlesae* no denticles are present posterolaterally, but some are present within the lingual furrow along the edge of the plate.

5. **A section of the dental plate** (Figs. 11–14) cut near the posteromedial part of the plate, shows the arrangement of the tooth plate, the prearticular and the Meckelian bone. This section passes from the about the mid-length of the adductor opening to the lingual cavity, but it is sufficiently central to be considered as typical of the tooth plate. The specimen was studied in an optical section and from a surface cut parallel to this one and studied by SEM. The optical section clearly shows the presence of irregular canals that probably represent the sites of activity of micro-organisms, possibly fungal hyphae. Such features are known in other sections made from *Dipnorhynchus* specimens found at Wee Jasper and Taemas.

Deep weathering of the plate occurs along the medial side of the section, and along the dental surface, but fortunately some of this weathering is outside the main area of tooth-plate development. Peculiarities of the tooth plate have been recognised by workers on *Dipnorhynchus* since White (1966: 7) made the following comments: "the lower jaws of *Dipnorhynchus sussmilchi* … do not shew tooth-plates with separate denticles but a crushing surface of raised blisters, large in extent but almost featureless, formed by a thickened layer of dentine continuous with the supporting bone." Clearly he thought that the material of the tooth-plate was dentine. The section accompanying that description (White, 1966: fig. 1) shows a cross section of the large rounded "blister" forming the posterior part of a tooth plate. The material referred to as "dentine" consists of long narrow tubes which extend to the surface of the tooth-plate, though some surface decomposition of the tissue took place before collection. No evidence of a basal pulp cavity is present. We have specimens of *D. kurikae* which show similar arrangements.

Naturally this kind of tooth-plate cannot grow in the same way as the plates of later dipnoans, because there is no addition of marginal teeth to permit lateral growth and no median suture to permit internal growth. Furthermore the blister-like tubercles on the plates of *D. sussmilchi* and *D. kurikae* increased their height and their palatal shape without being at the plate margin. Some of these blisters have a "botryoidal" appearance in oral view (Campbell & Barwick, 1985: figs. 8d, 9a) indicating that their buccal surfaces grew from several sites. In the absence of a pulp cavity, we must begin to be concerned that the material called "dentine" is not dentine of the kind as occurs in later dipnoans.

In *D. cathlesae*, the thin tubes of tissue forming the

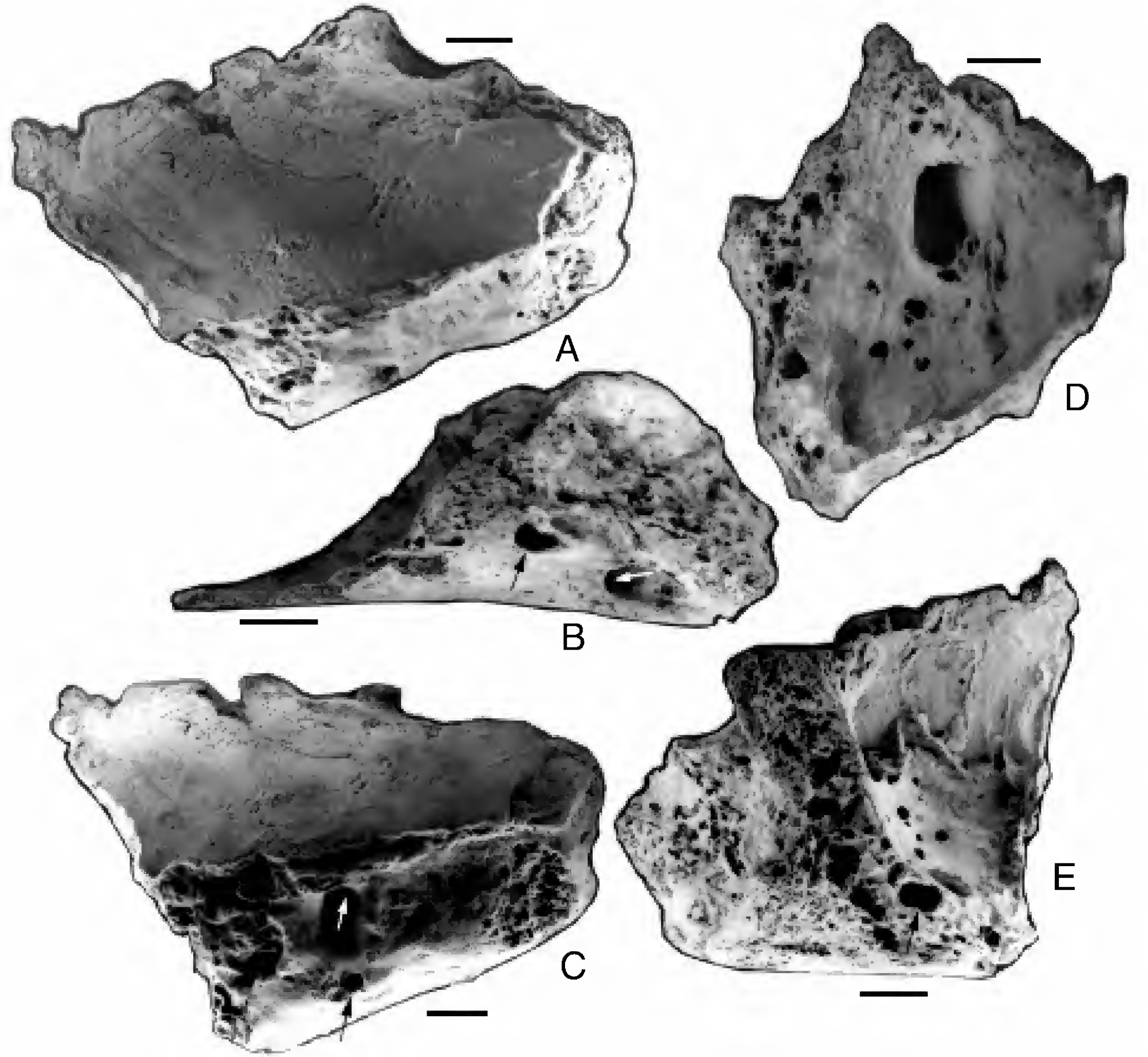


Figure 8. Views of the broken off fragment from the left corner of the specimen of *Dipnorhynchus cathlesae*. A, lateral view showing Westoll lines; B, dorsal view with the foramina for the ramus mandibularis V shown with a black arrow, and for the ramus mentalis externus VII shown with a white arrow; C, ventrolateral view showing the thick Meckelian bone with the large foramen for the ramus intermandibularis V shown with a white arrow, and a much smaller foramen for the ramus mentalis internus VII shown with a black arrow. The opposite end of the same canal is shown in E with a black arrow. D, E, two views of the internal surface showing the large foramen through which the nerves V and VII pass into the adductor chamber. Black arrow indicates the position of the ramus mentalis internus VII on the inner surface. Scales = 1 cm.

blisters have an irregular arrangement, but most of them are long and thin. A vertical section shows everything from longitudinal to transverse sections of the cavities. These cavities are filled with sediment, and some are branched. The walls are light coloured, but around the central canals is a darker layer. In several parts of the section, the hard tissue has strong concentric lines which indicates that recrystallisation has not taken place. These hard tissues should show dentine tubules, if the tubes are made of dentine, but in *D. cathlesae* no evidence of dentine tubules can be found, although it is clear that recrystallisation was **not** a factor in destroying fine structures. The absence of dentine tubules and the fact that reorganisation of the surface of the dental-plates took place merely by upward growth from preexisting bone, indicates that the tooth-plate grew by growth from the underlying bone. We deal with this problem in a publication on *D. kurikae* (Campbell & Barwick, in press).

The inner face of the prearticular is covered with bone of a different character. It is distinguished in thin section by layers of bone lying slightly oblique to the depositional surface, the layers being joined by short vertical struts. As shown on Figs. 11A,C, a thin layer without bone lies between this material and the prearticular. However, it is not continuous along the whole length of the section and it passes into lamellated bone at each end. We consider that

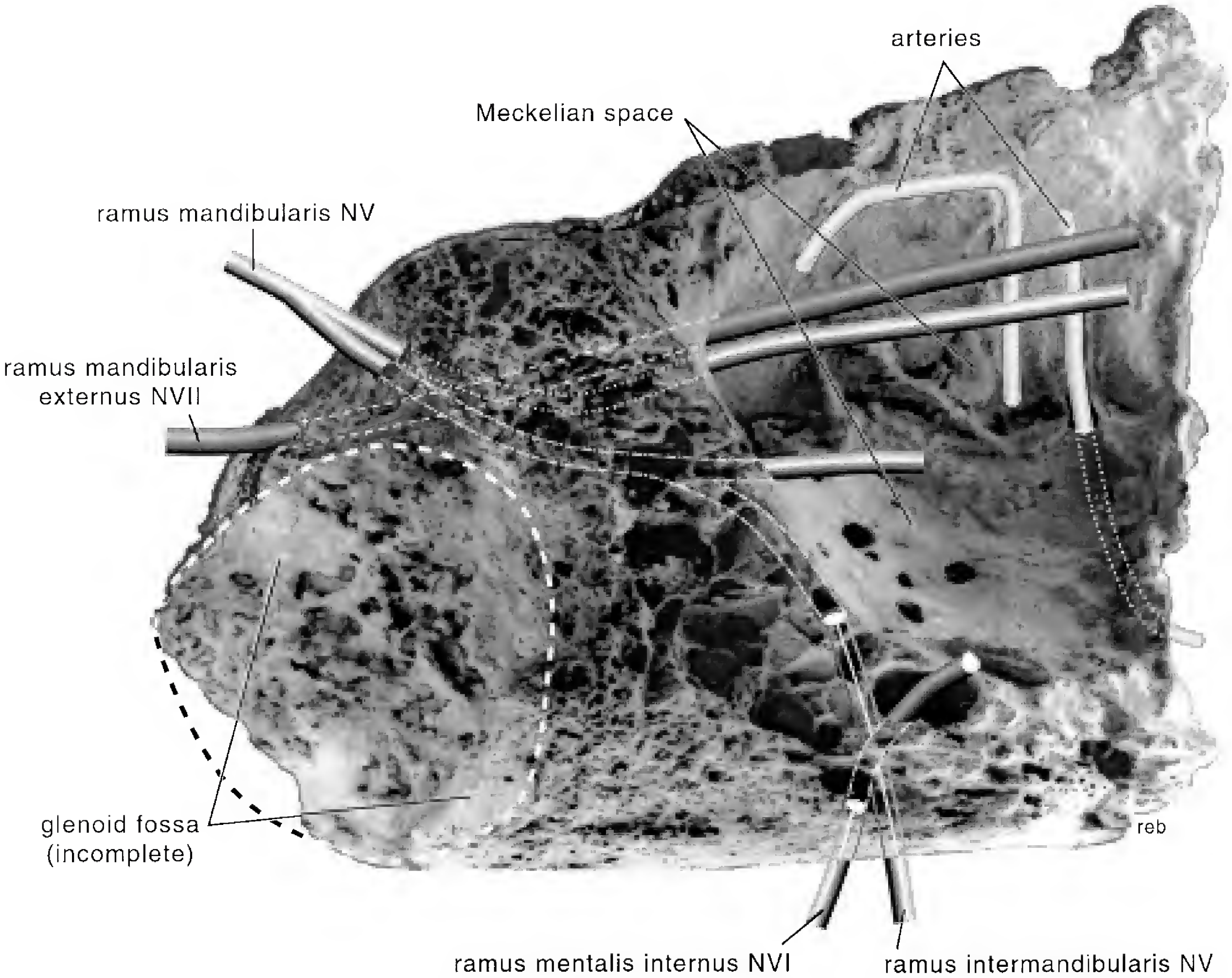

arteries
Meckelian space
ramus mandibularis NV
ramus mandibularis externus NVII
glenoid fossa (incomplete)
reb
ramus mentalis internus NVI
ramus intermandibularis NV

Figure 9. Reconstruction of the structures illustrated in Figs. 8D,E. Tubes buried in bone are indicated by broken lines. The glenoid is incomplete and is shown by a heavy dashed line. Two branches are shown for the ramus mandibularis nerve V whose paths are shown on the specimen. The internal branching of NV is well shown on the specimen. The arteries on the inner face of the surangular are shown by shallow grooves, and their paths are indicated.

the gap represents the sites of cells resorbing the Meckelian bone prior to deposition of new prearticular bone. The spaces between the bone layers are elongate. Optical sections show strong lines of growth parallel with the length of the lamellae, and these contain spaces which are also parallel with the lamellae (Figs. 11C, 12D, 14A). These are probably osteocyte spaces, and with the lamellar structure give an appearance which is quite different from that of the bone spaces in the prearticular bone. Is this bone a precursor of the prearticular, or is it a lining of Meckelian bone which occurs around the adductor chamber in other dipnoans? We know of no instance where a precursor of a dermal bone was laid down in bone which is so different in bone so different from the dermal bone itself. Observation of the interior of the adductor chamber shows that the layer runs forwards and around onto the external bone in the normal way that Meckelian bone does. Hence this seems the most appropriate name for the bone.

Between the thin-layered Meckelian bone and the main bone of the prearticular, there is a linear series of bone layers more widely separated than those in the Meckelian bone (Figs. 11A,C). These lines of bones are gradually disappear laterally towards the inner edge above the posterior face of the mandible. The separation of bony layers is greater than in the Meckelian layers, and the openings between the layers is more elongate and thicker. These inner layers give the appearance of older Meckelian bone layers which have been partly modified by later activity of bone deposition. We note also that these lamellae have a similar internal structure to the main Meckelian bone, and it is easily distinguished from the intergrown porous bone which invades it.

Meckelian bone was thickened along the surface bordering the adductor chamber as would be expected. The prearticular thickens by resorption of the inner surface of the Meckelian bone and replacement by vascular bone of the usual prearticular type. This is seen particularly well on Fig. 11C. The thickness and the laminated texture of the Meckelian bone are possibly to be explained by the magnitude of the adductor muscles which were attached to it.

This interpretation is supported by our observations on the specimens of *Chirodipterus australis* and *Holodipterus gogoensis* etched from the Gogo faunas. In those species

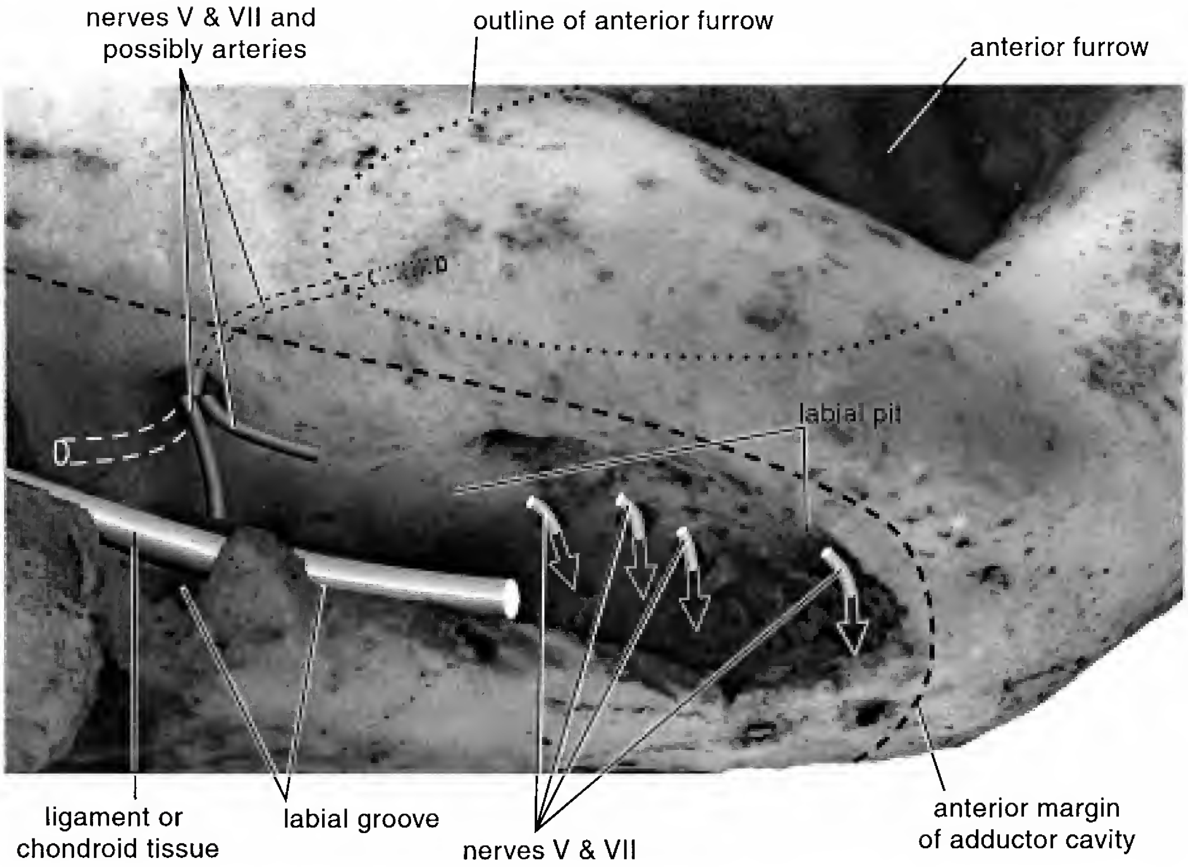

nerves V & VII and possibly arteries
outline of anterior furrow
anterior furrow
labial pit
ligament or chondroid tissue
labial groove
nerves V & VII
anterior margin of adductor cavity

Figure 10. Reconstruction of the right labial pit showing the passage of the ligament or the chondroid tissue from the adductor chamber to the labial pit; some of the nerves V and VII running from the adductor cavity to the labial pit; and the nerves V and VII running through the large foramen at the posterior end of the labial pit and also into the anterior furrow. Parts of the canals buried in the bone are shown with a linear symbol or with a dotted margins.

much of the adductor space is lined by a thin layer of Meckelian bone which continues anteriorly from the articular bone. A gap is left between the prearticular and the inner lining of the Meckelian bone, and this must have been filled by the Meckelian cartilage. The prearticular was able to expand inwards by occupying this space and replacing the cartilage. The thin lining of the bone around the adductor chamber must have been resorbed and redeposited during growth. In *D. cathlesae*, no space was left to be occupied by the Meckelian cartilage. The Meckelian bone against the adductor chamber was much thicker than in the other two species, and continued to grow inwards as the prearticular expanded into the space previously occupied by Meckelian bone. This arrangement is interesting because it confirms the view that little growth took place on the buccal layers of the prearticular, and hence the absence of tubercles (blisters) on the grinding surfaces. Most of the thickening of the prearticulars took place by the rapid inward growth, occupying space originally occupied by Meckelian bone.

6. The **glenoid fossa** (Figs. 3B, 4A, 6F, 9) is not well exposed on either side of the specimen, but parts of both the articular bones remain. We have recently discovered that in *D. kurikae*, the preglenoid process has a strong dorsally directed ligament attachment on its dorsal surface immediately inside the surangular. In *D. cathlesae* the surface of the articular in front of the glenoid fossa is flattened, and could have provided a surface for the attachment of a ligament. This surface is not extended forwards as a process plastered on the inner surface of the surangular on which ligaments could be attached, a feature found in other dipnorhynchids (Campbell & Barwick, 1985: figs. 8a, 9). Such a structure is exposed to weathering, and it could have been removed before collection of *D. cathlesae*. However, even if such a structure was not present, the articulation of the jaw would have been supported by the connective tissue forming the inner face of the glenoid region as shown in section 4 above. The matter will be further discussed in our paper on *D. kurikae*.

7. In dorsal view, the **adductor opening or fossa** (Figs. 3B, 4A, 6F) is pear shaped, being much wider posteriorly. Two cm from its posterior edge, it measures 4 cm across from crest to crest, and narrows gradually in front of that. This is a very different shape from the more parallel sided adductor opening in *D. kurikae*, in which the opening narrows down only within a short distance of the anterior end. In *D. cathlesae*, the lower medial wall of the adductor chamber formed by the inner face of the prearticular, is

very roughly ridged (Fig. 7C), almost to the anterior edge of the chamber. The coarse vertical ridges on the inner wall of the chamber extends much further forward than one would expect, reaching well up under the anterior furrow. Both sides of the specimen, but particularly the left, also have a few anteriorly directed ridges on the inner face of the outer wall of the chamber. On *D. kurikae* the ridging is not so powerful and does not extend so far up the inner face of the chamber. In *D. cathlesae* the adductor muscles were very strong and some of them were attached far forward of the anterior margin of the adductor opening, and on inner and outer sides of the adductor chamber.

In *D. kurikae*, the articular runs forwards along the edge of the prearticular on the upper edge of the adductor opening, making a distinct rounded ridge which shows so well in dorsal view. In *D. cathlesae*, the articular is present in this position, but it does not appear as a rounded ridge in dorsal view (Figs. 3B, 4A). The reason for this is that the prearticular rises high against the edge of the adductor chamber, and the articular is smoothed out against it rather than forming a rounded ridge. This feature is obviously related to the way in which the tooth plate comes to a crest along its lateral margin.

8. The **lingual furrow** (Figs. 4A,B) is slight, has an almost vertical lower face ventrally on the prearticulars, but turns over into a shallow groove dorsally. The lower vertical part is very high as compared with that of *D. kurikae*. The prearticulars forming the lateral parts of the front wall of the lingual cavity are thick, and they are deeply concave, overhung by a projection on the tooth plates.

The anterior space for the tongue is short and narrow, though the posterior part must have been wide. In the posterior face of the prearticular bone is a broad deep cavity into which the lateral parts of the tongue pad would have fitted. Judging from the position in extant dipnoans, the anterior part of the tongue would have been short, and would not have extended forwards into the space occupied ventrally by the rounded eminence in the median floor. The whole contour of this region indicates that the hyoid system would have been very posterior in position and would have had little opportunity to move dorsally and ventrally to control the buccal space. This emphasizes emphatically that the hyoid arch would not have been able to compress an air space in the back of the buccal cavity as would have been required for air breathing along the same lines as in extant dipnoans.

At their ventral edge on the posterior face of the mandible, where the prearticulars join the dermal bones, the prearticulars have a distinctive inturning towards the dermal bone. This leaves a flange around the specimen which is larger than any other species of the genus.

9. The **nerve canals** (Figs. 3B, 4A,B, 8, 9) lateral to the glenoid fossa are quite different on the two sides of the specimen. On the left, two large foramina lie between the articular and the surangular. The more posterior one is more laterally placed and passes posterodorsally into a deep groove which runs off the articular. It presumably contained a branch of the nerve ramus mentalis externus VII (*f me VII* of Thomson & Campbell, 1971). Note that Miles (1977: fig. 102) has two branches of this nerve in *Chirodipterus australis*, but he was unsure about the significance of this because the two did not appear in all specimens. Internally this large foramen in *D. cathlesae* opened after a short course into a large chamber. Within this chamber the courses of the furrows are not clear, but the VIIth nerve enters a groove which ran down the inner face of the surangular bone. The dorsal one is small and lies at the top of the foramen and cannot be traced anteriorly. The lateral one lies against the surangular and continues along the inner face of that bone.

The more anterior foramen on the left side of the dorsal surface of the bone is of about the same size as the posterior one, but it passes through the articular in a more dorsomedial orientation than the ramus mentalis externus (*f me VII* of Thomson & Campbell, 1971), into the same large internal chamber. On the external surface this groove seems to be entered by two foramina, the anterior one being dorsally and the lateral one being posterodorsally directed. Its position in the chamber and anterior to it is not clear on the specimen, but it sends a groove down the inner face of the chamber to run to the foramen intermandibularis V (see below) on the ventral surface of the mandible. The anterior opening of the chamber shows a rounded edge indicating that a branch of nerve V passed into the adductor chamber away from its walls, and hence into the adductor muscles. Up towards the dorsal foramen, another branch joins the groove that carries the ramus VII forwards along the surangular. We consider that it carried the mandibularis V along with the mandibularis VII to the anterior end of the mandible.

Opening ventrally out of the mandible is a large rounded foramen in the articular, rather than at the junction between the dermal bone and the articular. It would have transmitted the intermandibularis nerve V (*f int V* of Thomson & Campbell, 1971). In addition to the V nerve, we expect from the above description that it also contained branches of the VII nerve. As would have been expected, the grooves leave this foramen in anterior, ventral and posterior directions innervating the elongate intermandibularis muscle.

Ventral to this foramen for the ramus intermandibularis V nerve (*f int V* of Thomson & Campbell, 1971) is a much smaller foramen which connects through the articular below the floor of the adductor chamber in a much larger foramen on the broken internal surface. The right side of the specimen apparently had a similar structure, but it has been broken through during preservation. A similar foramen has been recorded by Miles (1977) in *Chirodipterus* which he labelled *cr.c*, and he indicated only that it was the "posterior cross canal". He did not indicate the function of this structure. Because of its position and the presence of small openings in its wall making connections with the surrounding bone, we consider that this system contained a nerve. The canal is in an appropriate position for the ramus mentalis internus VII nerve, according to the reconstructions of *Neoceratodus* by Fox (1965).

Miles (1977: 204) commented that he considered the mandibularis V nerve to have passed through the adductor fossa, and that "all the openings in this region, in both *Dipnorhynchus* and *Chirodipterus* transmitted branches of the *R. mentalis externus VII*". Our specimen shows that the nerve V would not have passed in this way; indeed some of our specimens of *C. australis* indicate the same point. It

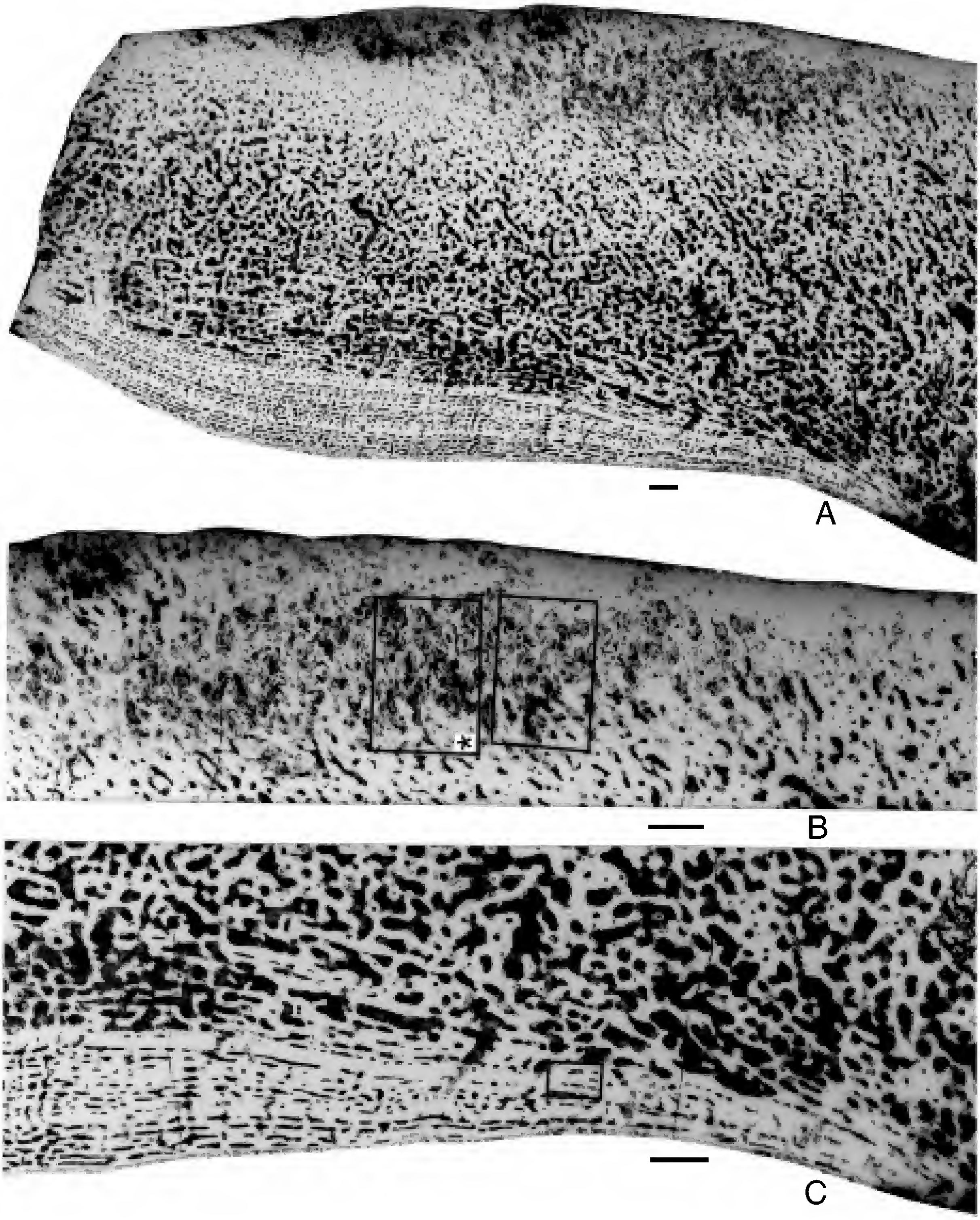


Figure 11. Sections of the prearticular of *Dipnorhynchus cathlesae*. A, transverse section as shown by the black arrow on Fig. 3B. The left side is towards the adductor fossa, and the right onto the posterior wall of the mandible. A thin layer of sediment is left attached to the base of the section. A, shows the Meckelian bone at the base overlain by thin layers of Meckelian bone being transformed into prearticular bone. At the top is a change in texture where the prearticular is replaced by so-called "dentine". The boundary between the two tissues is marked by discontinuities. The topmost part of the section is so weathered that no detail can be seen in it. B, enlargement of the top of A showing the contact between the main bone of the prearticular and the so-called "dentine". The uppermost surface is weathered. C, enlarged part of the Meckelian bone and contact with the prearticular. Note how the layers in the laminae change abruptly to become less continuous in the prearticular. Scales = 1 mm.

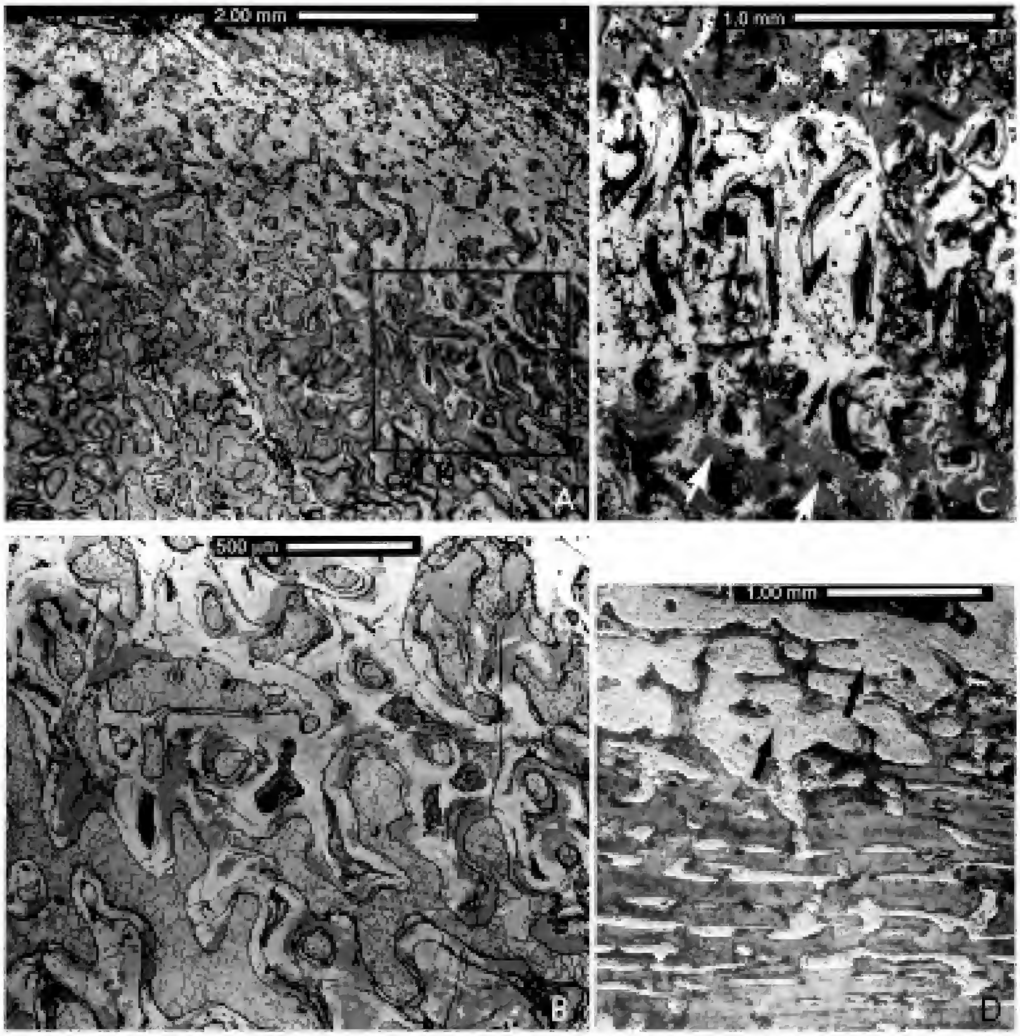


Figure 12. A–C, back scattered SEM figures taken from a slice cut parallel with the section in Fig. 11. A, shows the transition between the dark coloured bone at the base and the lighter coloured so-called "dentine" at the top. B, enlargement of the area shown on A. Note the absence of any continuous gap between the two types of tissue. The crazed pattern is calcite infilling the specimen. C, specimen of the tissue near the top of the section showing the elongate spaces in the so-called "dentine" (black arrow), and the bone at the base (white arrows). D, section through the Meckelian bone showing lamination and the abundance of elongate osteocyte spaces. Note the transition from the closely layered Meckelian bone at the base into the overlying bone. Black arrows indicate calcite infillings of the matrix.

will be obvious that we consider the complication suggested by Miles to be unnecessary, and that Thomson & Campbell (1971) were correct in having both nerves V and VII oriented as they suggested.

On the right posterodorsal side of *D. cathlesae*, there is a single opening which is larger than either of the nerve openings on the left side of the specimen. The inner wall of this opening has a ridge which separated the two nerves entering the foramen. The posterior opening is by far the smaller one and the more dorsal opening is almost vertical. We consider that these are for the ramus mentalis externus VII and the ramus mandibularis V respectively. The internal cavity within the articular is smaller than the one on the other side, and its anterior opening is also smaller.

10. The **infradentary bones** (Figs. 3A, 5, 6B) are moderately well exposed, especially on the right side of the specimen. They were originally covered with cosmine, but wear has removed some of that tissue. On the right side the posterior part of the surangular is exposed. It has an acute posterior end which rises high on the side of the mandible and lies immediately beneath the foramen for the ramus mentalis externus VII. This is unusually high in comparison with *D. kurikae* and *D. sussmilchi*, in which a granulated surface occupies the upper part of the bone.

Westoll lines are obvious on the surangular on the left side (Figs. 8A,C). They close posteriorly where they turn upwards slightly to produce a banana shape. The ventral edge of the surangular is exposed incompletely on the right side of the specimen, and gives the impression that the bone runs forward to the ventral edge of the labial pit, though its anterior edge cannot be seen. This is appropriate for a dipnorhynchid, in which the surangular is always long. On the right side the lateral line canal is visible lying about half way down the bone.

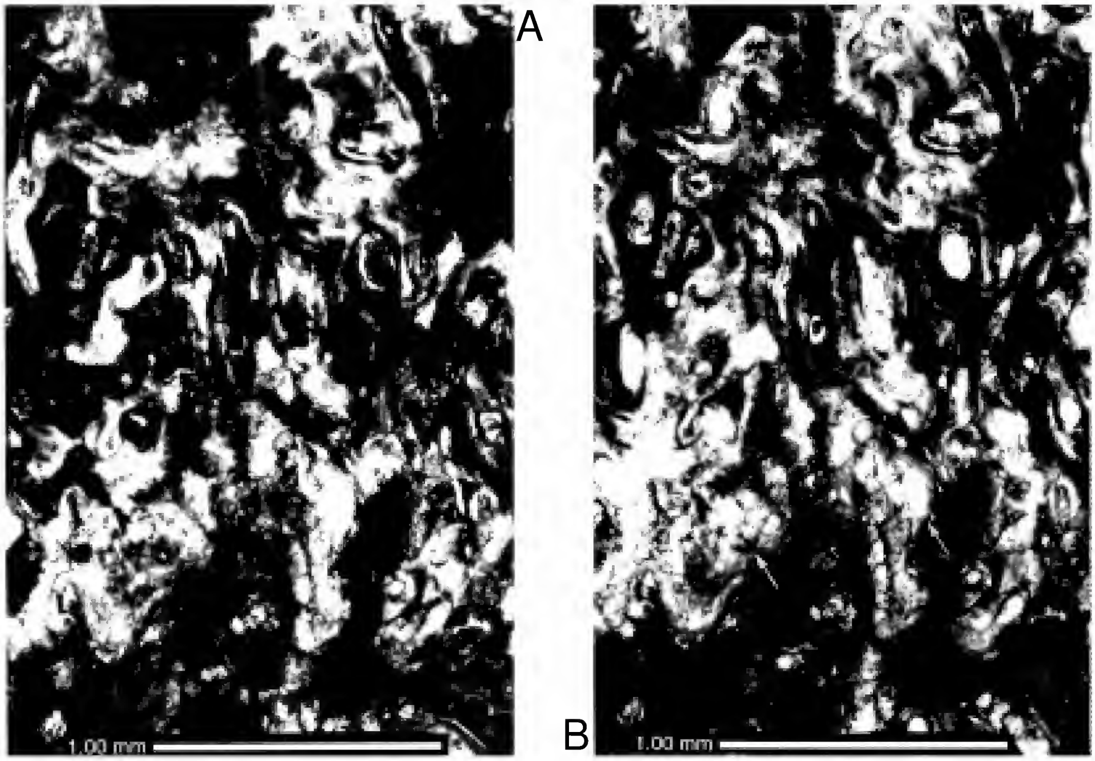


Figure 13. Two views of the one position of the optical section outlined in Fig. 11B marked with an asterisk. A, crossed polarised light and B, single polarised light. At the base the tissue is prearticular bone, and at the top it is the so-called "dentine". The large areas marked with the white arrows are infillings of the open spaces between the bone and the so-called "dentine".

11. Because the **posterior edges of the infradentaries** (Fig. 6A) are badly worn, it is not possible to give precise positions for all the foramina which usually occur along the line between the infradentaries on the one hand, and the prearticulars and the Meckelian bone on the other. In *D. kurikae*, the largest foramen along this line is figured by Campbell & Barwick (1985: fig. 8B), but it was unlabelled. Several other topotypes of *D. kurikae* have since become available, and all show this feature. *Dipnorhynchus sussmilchi* has a smaller foramen in this position, and one or two other foramina medial to it. The specimen of *D. cathlesae* is poorly preserved in this region on both sides of the specimen, but on the left side the broken surface shows a large foramen passing between the Meckelian bone and the infradentaries. It is a section across a canal which continues forward and enters the adductor chamber in a forwards position. This is in the same position as the foramen in *D. kurikae*, and the foramen for the efferent branchial artery in *D. sussmilchi* (Thomson & Campbell, 1971: fig. 22).

Specimens of *D. sussmilchi* show strong canals on the face of the prearticular in the adductor chamber (Thomson & Campbell, 1971: figs. 47–49). These develop from a foramen which lies between the postsplenial and the prearticular. A similar groove is found in *D. cathlesae* running up the surface through the bone forming the coarse ridges used for muscle attachment, then across the under surface of of the dental plate and then into a fossa in the plate at the level of the anterior end of the adductor fossa. It enters a deep tube in the plate, and can be traced through the plate in an anterior direction, emerging in the posterior corner of the anterior pit. Further back along this main canal where a sharp turn forwards occurs, a weaker canal runs forward along the line indicated by the symbol *sa1* by Thomson & Campbell (1971: fig. 22). The more posterior branch of the canal running to f_l *sa 1* in *D. sussmilchi* is not well represented on our specimen, mainly because the specimen is poorly preserved in that region.

We point out that the canals as in *D. sussmilchi* have now been found in new specimens of *D. kurikae* and in *D. cathlesae*. No matter how we interpret these structures in functional terms, it is clear that they are features found in all dipnorhynchids.

Comparisons

In the above description we have concentrated on comparisons with *D. kurikae*, which is the species stratigraphically closest to *D. cathlesae*, and also occurs in the Wee Jasper sequence. The only other species in which the mandible is known is *D. sussmilchi*, the type species. This was described by Thomson & Campbell (1971). Since that time we have discovered three imperfect specimens of *D. sussmilchi* in the *Spinella yassensis* Limestone, some of which allow us to add to the previous description.

In *D. sussmilchi* the lingual furrow is deeper and proportionately narrower than that of *D. kurikae*. It continues forward as a distinct furrow to the anterior furrow which lies just medial to and slightly behind the end of the

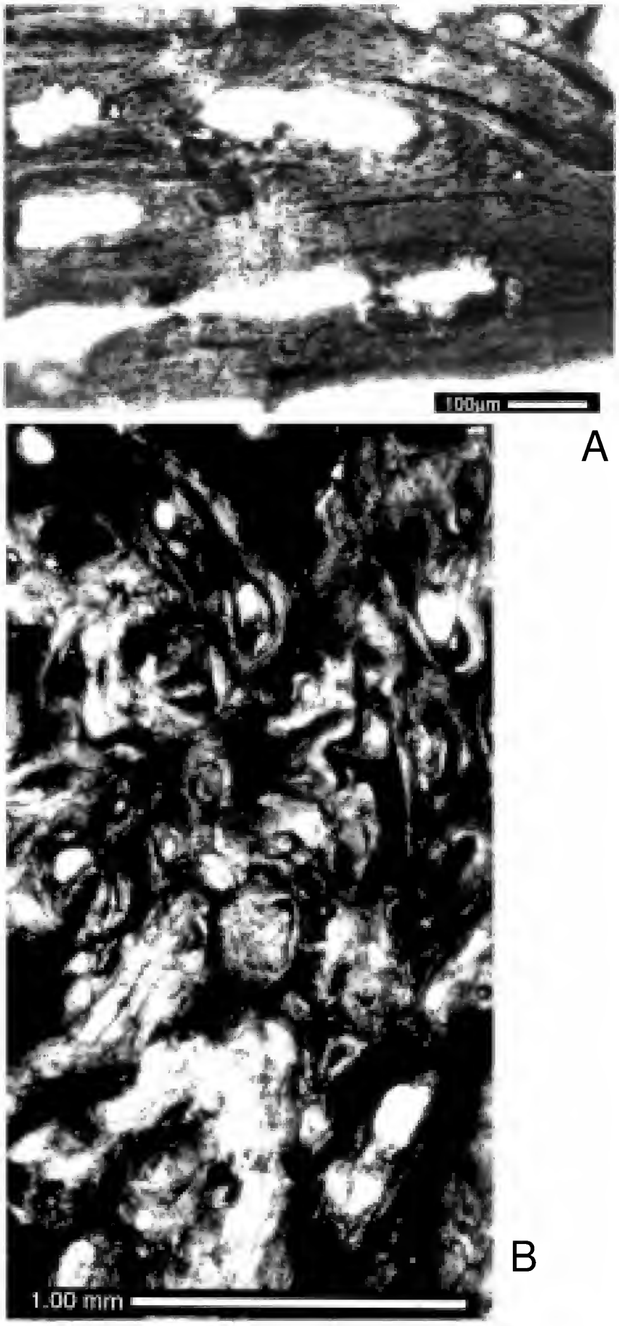


Figure 14. A, enlarged part of the Meckelian bone (outlined on Fig. 11C). It shows the lamination and the abundant osteocyte spaces. B, section under crossed polars. Its position is the right rectangle shown on Fig. 11B. It crosses the boundary between the prearticular bone at the base and the so-called "dentine" at the top. The two images are reversed in comparison with Fig. 11.

anterior furrow. Posterior to this is a deep groove, the inner edge of which is well defined by a ridge that extends back to the large rounded posterior protuberance forming the main grinding face of the tooth plate. In all these features, *D. sussmilchi* is unlike *D. kurikae*, and even less like *D. cathlesae*. Like *D. kurikae, D. sussmilchi* has a similar groove running between the lateral margin of the tooth plate and the posterior protuberance. We have also noticed that the articular has a projection in front of the glenoid fossa to which was attached a muscle as in *D. kurikae*. This is not present to anything like the same extent on *D. cathlesae*. Finally, the lip pit on *D. sussmilchi* has a well-rounded anterior edge and does not extend into a furrow as in the other species.

ACKNOWLEDGMENTS. This work has been supported by a Small ARC Grant. We are grateful to Ian and Helen Cathles for permitting us to describe the specimen. Ken and Sally Kilpatrick of Taemas Station helped with the excavation of the specimen. The SEM work was done by Dr Roger Heady of the SEM Unit, ANU.

References

Basden, A., C.J. Burrow, M. Hocking, R. Parkes & G.C. Young, 1999. Siluro-Devonian microvertebrates from south-eastern Australia. In *IGCP Project 328, Final Report*, eds. A. Blieck & S. Turner. Courier Forschungs—Institut Senckenberg.

Bemis, W.E., 1987. Feeding systems in living Dipnoi: anatomy and function. *Journal of Morphology Supplement* 1: 247–275.

Campbell, K.S.W., & R.E. Barwick, 1984. *Speonesydrion*, an Early Devonian dipnoan with primitive tooth plates. *PalaeoIchthyologia* 2: 1–48.

Campbell, K.S.W., & R.E. Barwick, 1985. An advanced dipnorhynchid lungfish from the Early Devonian of New South Wales, Australia. *Records of the Australian Museum* 37: 301–316.

Campbell, K.S.W., & R.E. Barwick, (in press). New information on the Early Devonian lungfish *Dipnorhynchus kurikae* from Wee Jasper, New South Wales.

Fox, H., 1965. Early development of the head and pharynx of *Neoceratodus* with a consideration of its phylogeny. *Journal of Zoology (London)* 146: 470–554.

Garratt, M.J., & A.J. Wright, 1989. Late Silurian to Early Devonian biostratigraphy of southeastern Australia. In *Devonian of the World*, eds. N.J. McMillan, A.F. Embry & D.J. Glass. *Canadian Society of Petroleum Geologists, Calgary Memoir* 14(3): 647–662.

Hill, D., & J.S. Jell, 1970. The tabulate coral families Syringolitidae Hinds, Romeriidae Pocta, Neoreomeriidae Radugin, and Chonostegitidae Lecompte, and Australian species of *Romeripora* Kraicz. *Proceedings of the Royal Society of Victoria* 83(2): 171–190.

Jaekel, O., 1927. Der Kopf der Wirbeltiere. *Zeitschrift für Anatomie und Entwickelungs geschichte* 27: 811–974.

Miles, R.S., 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61: 1–328.

Pedder, A.E.H., J.H. Jackson & G.M. Philip, 1970. Lower Devonian stratigraphy in the Wee Jasper region of New South Wales. *Journal of Paleontology* 44(2): 195–251.

Thomson, K.S., & K.S.W. Campbell, 1971. Structure and relationships of the primitive Devonian lungfish *Dipnorhynchus sussmilchi* (Etheridge). *Bulletin of the Peabody Museum of Natural History* 38: 1–109.

White, E.I., 1966. Presidential Address: A little on lung-fishes. *Proceedings of the Linnean Society of London* 177: 1–10.

Manuscript received 28 December 1998, revised 18 March 1999 and accepted 19 March 1999.

Associate Editor: G.D. Edgecombe.

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 141–160. ISSN 0067-1975

Monophyly, Interrelationships and Description of Three New Genera in the Dottyback Fish Subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae)

ANTHONY C. GILL [1] AND ALASDAIR J. EDWARDS [2]

[1] Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom
t.gill@nhm.ac.uk

[2] Centre for Tropical and Coastal Management Studies, Department of Marine Sciences and Coastal Management, University of Newcastle, Newcastle upon Tyne NE1 7RU, United Kingdom
a.j.edwards@newcastle.ac.uk

ABSTRACT. Within the Pseudochromidae, the subfamily Pseudoplesiopinae is diagnosed by six unequivocal autapomorphies: single tubed lateral-line scale; posterior part of pelvic bone with triangular or hook-shaped lateral process; base of anterior process on pelvic bone posteriorly positioned; coracoid articulates ventrally with medial face of lateral lamina of cleithrum; basihyal bound to anterior face of basibranchial 1; and urohyal with prominent dorsally directed process. Five genera are recognised in the subfamily. *Pseudoplesiops* Bleeker (*Nematochromis* Weber is a junior synonym), with seven nominal species, is diagnosed by a single autapomorphy: medial laminae of pelvic bones expanded dorsally. *Chlidichthys* Smith (*Wamizichthys* Smith is a junior synonym), with 10 nominal species, is diagnosed by two autapomorphies: lower lip incomplete; and second infraorbital bone absent. *Pectinochromis* n.gen. (type species *Pseudoplesiops lubbocki* Edwards & Randall), with a single nominal species, is diagnosed by five autapomorphies: second dorsal-fin pterygiophore inserting between neural spine 3 and 4; second supraneural bone absent; first dorsal-fin pterygiophore expanded anteriorly; first dorsal-fin pterygiophore with lateral processes; and gill rakers relatively numerous. *Amsichthys* n.gen. (type species *Pseudoplesiops knighti* Allen), with a single nominal species, is diagnosed by a single autapomorphy: upper preopercular pore usually absent. *Lubbockichthys* n.gen. (type species *Pseudoplesiops multisquamatus* Allen), with a single nominal species, is diagnosed by four autapomorphies: scales small; scales cycloid at all stages of ontogeny; some head bones with weakly honeycombed surface; and parietal enclosing dorsal part of supratemporal laterosensory canal. A parsimony analysis of various characters of the laterosensory system, caudal skeleton, dorsal-fin osteology, and fin-ray branching supports the following relationships: (*Lubbockichthys* ((*Amsichthys* + *Pseudoplesiops*) (*Chlidichthys* + *Pectinochromis*))).

GILL, ANTHONY C., & ALASDAIR J. EDWARDS, 1999. Monophyly, interrelationships and description of three new genera in the dottyback fish subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudochromidae). *Records of the Australian Museum* 51(2): 141–160.

The Pseudochromidae is a family of small, reef-associated fishes, which are distributed throughout the Indo-Pacific. The family is currently divided into four subfamilies: Anisochrominae, Congrogadinae, Pseudochrominae and Pseudoplesiopinae (Godkin & Winterbottom, 1985). The objectives of the present paper are to provide evidence for monophyly of the Pseudoplesiopinae, to diagnose its included genera, and to investigate phylogenetic relationships among those genera. Species-level revisions of the genera will be provided in forthcoming papers by the present authors.

Historical review of the systematics of the Pseudoplesiopinae

Bleeker (1858) described the genus *Pseudoplesiops* for a new species, *P. typus*, from a single specimen from Goram (= Manawoka), Indonesia. He assigned it to his family Pseudochromides [sic], noting that it fell between *Pseudochromis* Rüppell and *Plesiops* Oken (now Plesiopidae) in morphology. He described it as having: dorsal fin with 16 unbranched and nine or 10 branched rays; anal fin with seven unbranched and nine branched rays; pelvic fin with no spine and five rays, the outer two elongate and filiform; palatine teeth absent; scales cycloid; and a single anterodorsal lateral line consisting of inconspicuously pored scales. He later (Bleeker, 1875) reported on an additional specimen of the species from Ambon (actually referable to a new *Pseudoplesiops* species, which we will describe elsewhere) and included the species as sole member of the Pseudoplesiopini, one of three groupings he recognised within his family "Pseudochromidoïdes." The remaining two groupings were Cichlopini, for *Cichlops* Müller & Troschel (= *Labracinus* Schlegel), *Pseudochromis* Rüppell, *Pseudogramma* Bleeker (now in Serranidae), *Gramma* Poey (now in Grammatidae) and *Trachinops* Günther (now in Plesiopidae), and Plesiopini for *Plesiops* Oken and *Paraplesiops* Bleeker (both now in Plesiopidae).

Günther (1860) assigned *Pseudoplesiops* to his Pseudochromides, which he treated as a subgroup of the Trachinidae, along with *Pseudochromis, Cichlops, Opisthognathus* [sic] Cuvier (now Opistognathidae), *Notothenia* Richardson (now Nototheniidae), *Harpagifer* Richardson (now Harpagiferidae), *Heterostichus* Girard (now Clinidae) and *Pegetodes* Richardson (now Channichthyidae).

Boulenger (1895: 336) listed *Pseudoplesiops* in the Serranidae and noted that it "appears to combine characters of *Callanthias* [now in Callanthiidae] and *Plesiops*." Boulenger did not comment on the position of *Pseudochromis* and *Cichlops* in this paper, but later (Boulenger, 1901) placed them and genera now assigned to the Opistognathidae, Malacanthidae and Bathymasteridae in the Pseudochromidae.

Boulenger (1899) apparently overlooked Bleeker's (1858) use of *Pseudoplesiops* (despite his own 1895 reference to *Pseudoplesiops* Bleeker) and described *Pseudoplesiops* as a new genus for a new species of cichlid from the Congo, *P. nudiceps*. He later (1902) described another new species in the genus from the Congo, *P. squamiceps*. Pellegrin (1904) noted that *Pseudoplesiops* Boulenger was preoccupied and proposed a replacement name, *Nanochromis* (often subsequently misspelt *Nannochromis*).

Regan (1913) classified *Pseudoplesiops* in its own family, Pseudoplesiopidae, but included *Pseudochromis* and *Cichlops* in the Serranidae.

Weber (1913) described a new genus and species, *Nematochromis annae*, from two syntypes collected in Indonesia during the Siboga Expedition, one from Sarasa Island, Postilon Islands, and the other from Solor Strait. He described the species as having: dorsal and anal fins with two weak spines and mostly undivided, segmented rays, totalling 26–27 and 15 rays, respectively; pelvic fin with a weak spine and three unbranched, segmented rays; and lateral line interrupted, consisting of an anterodorsal series of 30 grooved scales and a midlateral posterior series of 15 grooved scales. He assigned the species to the Pseudochromidae.

Jordan (1923) provided a classification for nominal fish genera. He included only *Pseudoplesiops* in the Pseudoplesiopidae, retaining *Nematochromis* in the Pseudochromidae.

Weber & de Beaufort (1929) reexamined the holotype of *Pseudoplesiops typus* and modified some of the characters given by Bleeker (1858). Most notably, they reported in the generic diagnosis that the pelvic fin had I,4 rays, the first segmented ray thickened, produced and bifid, but reported in the species diagnosis that all segmented rays are simple, and that the anterior two are thickened and elongate. Weber & de Beaufort (1929, 1931) generally followed Regan's (1913) classification, but recognised the Pseudochromidinae [sic] as a serranid subfamily containing *Nematochromis, Dampieria* Castelnau (= *Labracinus*), *Pseudochromis* and *Pseudogramma*.

Berg (1940) also followed Regan's assignment of *Pseudoplesiops* to its own family, while retaining "pseudochromids" in the Serranidae.

Fowler (1931) recognised three subfamilies within the Pseudochrominae: Pseudogramminae (*Pseudogramma*); Pseudochrominae (*Dampieria, Pseudochromis* and *Nematochromis*); and Pseudoplesiopsinae [sic] (*Pseudoplesiops*). He later (Fowler, 1934) described two new monotypic pseudoplesiopine genera, *Loxopseudochromis* and *Opsipseudochromis*, from the Philippines.

Schultz (1943) described a new species, *Pseudoplesiops rosae*, from Rose Island, Phoenix Islands. He compared it with *P. typus* and assigned *Pseudoplesiops* to the Pseudochromidae, along with *Pseudochromis, Plesiops, Aporops* Schultz (now Serranidae) and *Pseudogramma*. He later (Schultz, 1953) synonymised *Nematochromis* with *Pseudoplesiops* and described an additional two species in the genus, *P. revellei* and *P. sargenti*. He also included acanthoclinids (now assigned to the Plesiopidae; see Mooi, 1993) in the Pseudochromidae.

Smith (1953) briefly described a new genus and species, *Chlidichthys johnvoelckeri* from east Africa. In the following year he reviewed pseudoplesiopsine [sic] fishes from south and east Africa (Smith, 1954). He ignored his previous description and described *C. johnvoelckeri* again as a new genus and species, along with another new congener, *C. pembae*, and a second new genus and species, *Wamizichthys bibulus*. He also assigned *P. rosae* to *Chlidichthys*, and, in comparing *C. pembae* with similar species, noted that: "It will not be surprising if a careful examination of *Pseudoplesiops typus* Bleeker, and of *Nematochromis annae* Weber, prove them to be one and the same and identical with the above." He excluded Fowler's (1934) *Loxopseudochromis* and *Opsipseudochromis* to the Owstoniidae (now considered a synonym of the Cepolidae; see Gill & Mooi, 1993: 331).

Smith (1954) separated the Pseudoplesiopsinae from the Pseudochrominae, the only other pseudochromid subfamily he recognised, on the basis of the following characters: dorsal- and anal-fin spines weak and flexible (versus strong); most segmented rays in dorsal and anal fins simple (versus mostly or all branched); pelvic fins with a weak spine and three or four simple, segmented rays (versus with a spine and five branched, segmented rays); lateral line reduced to a tubed scale at the shoulder and at most a series of pitted scales along middle of side and peduncle (versus represented by an anterodorsal and a posterolateral series of tubed scales); dorsal and anal fins without basal scaly sheaths (versus with basal scaly sheaths); lower pectoral-fin proximal radial abutting against both coracoid and scapula (versus coracoid only); and vertebrae 11 + 16 (versus 10 + 16).

Böhlke (1960) recognised three separate families, Pseudochromidae, Anisochromidae and Pseudoplesiopidae, and included *Chlidichthys, Nematochromis, Pseudoplesiops* and *Wamizichthys* in the latter.

Norman (1966) included *P. typus* as sole member of the Pseudoplesiopinae, which he regarded as a subfamily of the Plesiopidae. He recognised the Pseudochrominae as a subfamily of the Serranidae, in which he placed *Nematochromis* [as well as *Pseudochromis, Dampieria, Nesiotes* De Vis (= *Cypho* Myers), *Pseudochromichthys* (= *Plesiops*, Plesiopidae; see Mooi, 1996), *Pseudocrenilabrus* Fowler (now in Cichlidae), *Pseudogramma* and *Gramma*].

Lubbock reviewed pseudochromids of the Red Sea and northwestern Indian Ocean (Lubbock, 1975), central Indian Ocean (Lubbock, 1976) and western Indian Ocean (Lubbock, 1977). He recognised a total of nine pseudoplesiopine species in these papers, six of which he described as new. He placed all of the species in *Chlidichthys*, including the monotypic *Wamizichthys*.

Springer *et al.* (1977) synonymised the Anisochromidae with the Pseudochromidae, and proposed that the Anisochromidae and Pseudoplesiopinae were more closely related to each other than either was to the Pseudochrominae. Springer *et al.* noted that several of Smith's (1954) pseudoplesiopine characters were shared with anisochromines, and were thus synapomorphies of the two subfamilies (fin spine development; reduction in number of pelvic-fin rays; presence of at least one unbranched pelvic-fin ray; absence of scale sheaths on dorsal and anal fins; and absence of tubed scales in posterolateral lateral line). They diagnosed the Pseudoplesiopinae by the following autapomorphies: all segmented pelvic-fin rays simple; segmented dorsal-fin rays mostly simple; single tubed lateral-line scale; ventralmost proximal radial of pectoral fin articulates with coracoid and scapula; and all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials.

Edwards & Randall (1983) placed *Chlidichthys* in junior synonymy with *Pseudoplesiops*, and described a distinctive new species from the Red Sea, *Pseudoplesiops lubbocki*.

Godkin & Winterbottom (1985) provided evidence for classification of the Congrogadidae, previously placed in the Blennioidei or Trachinoidei, as a subfamily of the Pseudochromidae, and the sister-group of the Anisochrominae; they proposed that the Pseudoplesiopinae is the sister-group of the Anisochrominae + Congrogadinae. In so doing, they noted that all of the synapomorphies proposed by Springer *et al.* (1977) to unite the Anisochrominae with the Pseudoplesiopinae were also found in the Congrogadinae. They also noted that one of the characters used by Springer *et al.* to diagnose the Pseudoplesiopinae was also found in the Congrogadinae (all or almost all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials), and that another was not found universally among pseudoplesiopines (ventralmost proximal radial of pectoral fin articulates with coracoid and scapula). They therefore concluded that only three of the pseudoplesiopine autapomorphies proposed by Springer *et al.* (1977) were valid: segmented pelvic-fin rays all simple; most segmented dorsal-fin rays simple; and a single tubed lateral-line scale. However, they overlooked that *Pseudoplesiops lubbocki* Edwards & Randall (1983) has mostly branched dorsal-fin rays.

Allen (1987) described three new species in the genus *Pseudoplesiops*: *P. multisquamatus, P. knighti, P. howensis*. He noted, however, that they exhibited characters that had been traditionally used to separate *Chlidichthys* from *Pseudoplesiops*. He therefore regarded the generic assignment of the three species provisional.

Gill *et al.* (1991) followed Schultz (1953) in placing *Nematochromis* in synonymy with *Pseudoplesiops*. They noted that the syntypes of *N. annae* represent two different, and otherwise undescribed, species. They therefore designated a lectotype for *N. annae*, and described the second species, *P. collare*, based on the paralectotype and an additional specimen (holotype) from Flores. They also noted that Schultz's *P. sargenti* is a junior synonym of *P. typus*.

Gill & Randall (1994) demonstrated monophyly for *Chlidichthys* (including all of the Red Sea and western and central Indian Ocean species recognised in Lubbock's papers) from synapomorphies associated with lower-lip and cephalic-laterosensory morphology, and described a new species from southern Oman, *C. cacatuoides*. They noted that *Pseudoplesiops lubbocki* was not referable to *Pseudoplesiops*, and that instead it shared some characters with *Chlidichthys*. They suggested that it should be placed in its own genus.

Materials and methods

Phylogenetic analyses were performed using the implicit enumeration option of Hennig86 version 1.5 (Farris, 1988). Character polarity was determined by outgroup comparison. The Anisochrominae + Congrogadinae were used as first outgroup following the scheme of relationships proposed by Godkin & Winterbottom (1985). *Assiculoides desmonotus* Gill & Hutchins and *Assiculus punctatus* Richardson were used as the second and third outgroups, respectively. Although both of these genera are currently classified in the Pseudochrominae, current evidence indicates that they form successive sister groups to a clade consisting of the Anisochrominae + Congrogadinae + Pseudoplesiopinae (Gill & Hutchins, 1997: 45).

Nomenclature of head pores follows Winterbottom (1986). When referring to fin rays, the term ray is used in its general sense to include both spinous (azygous, unsegmented, bilaterally fused) and soft rays.

Numerous pseudoplesiopine specimens and radiographs were examined for external (including superficial osteology) and post-cranial axial skeleton characters, respectively. These materials, which represented all known species, will be listed in our forthcoming generic revisions. Similarly, a more extensive listing of pseudochromine and non-pseudochromid specimens will be listed in a forthcoming paper on pseudochromid phylogeny and biogeography by the first author. The following cleared and stained pseudoplesiopine specimens (variously prepared following the methods of Taylor, 1967, Dingerkus & Uhler, 1977, and Potthoff, 1984) were examined (institutional codes follow Leviton *et al.*, 1985): *Amsichthys knighti*, AMS I.22612-034 (1: 28.3 mm SL), AMS I.21540-046 (3: 19.5–30.4 mm SL), ASIZ uncat. (2: 24.0–27.4 mm SL), USNM 306590 (1: 29.2 mm SL); *Chlidichthys* sp. 1, ROM uncat. (RW 88–15) (2: 33.5–38.1 mm SL); *C. auratus*, USNM 211780 (2: 37.5–37.8 mm SL); *C. bibulus*, BPBM 27310 (1: 26.8 mm SL); *C. cacatuoides*, BMNH 1994.4.19.1 (1 paratype: 37.2 mm SL); *C. inornatus*, AMS I.23653-002 (1: 27.9 mm SL), ROM CS857 (3: 30.0–37.0 mm SL); *C. johnvoelckeri*, CAS 35451 (2: 24.7–37.9 mm SL), ROM uncat. (RW 88–26) (2: 36.2–38.7 mm SL); *C. pembae*, ROM uncat. (RW 88–15) (2: 21.2–23.3 mm SL); *C. rubiceps*, USNM 211777 (5: 12.0–15.0 mm SL), BMNH 1999.1.14.18 (1: 27.2 mm SL); *Lubbockichthys* sp. 1, AMS I.25107-067 (1: 47.3 mm SL); *L.* sp. 2, AMS I.39406-001 (1: 44.6 mm SL); *L.* sp. 3, AMS I.39407-001 (1: 37.2 mm SL); *L. multisquamatus*, AMS I.20779-175 (1: 36.3 mm SL); *Pectinochromis lubbocki*, BPBM 28119 (1 paratype: 35.5 mm SL); *Pseudoplesiops* sp. 1, AMS I.20756-014 (1: 25.7 mm SL); *P.* sp. 2, BMNH 1999.1.14.17 (1: 22.6 mm SL); *P. annae*, AMS I.21918-017 (1: 21.0 mm SL), USNM 270268 (2: 24.2–29.3 mm SL); *P. howensis*, AMS I.19755-024 (1: 21.0 mm SL); *P. rosae*, AMS I.22582-034 (3: 17.2–22.0 mm SL), BMNH 1999.1.14.14-16 (3: 18.0–21.4 mm SL); *P. typus*, AMS I.19442-013 (1: 50.6 mm SL), ROM CS585 (1: 49.0 mm SL). Our discussions of the morphology of immediate outgroups are largely based on details provided by Springer *et al.* (1977), Godkin & Winterbottom (1985) and Winterbottom (1986, 1996), and on the following cleared and stained specimens: ANISOCHROMINAE: *Anisochromis kenyae*, RUSI 4906 (1: 23.3 mm SL); *A. straussi*, USNM 215859 (4 paratypes: 19.0–24.0 mm SL), USNM 257761 (1: 8.0 mm SL). CONGROGADINAE: *Blennodesmus scapularis*, AMS I.26723-087 (2: 49.7–54.1 mm SL), BMNH uncat. (1: 29.6 mm SL); *Congrogadus spinifer*, BMNH 1911.1.4.3-4 (1: c. 122 mm SL); *Congrogadus subducens*, AMS I.26723-051 (1: 49.3 mm SL), AMS I.26723-052 (1: 18.7 mm SL), AMS I.26723-057 (1: 135.0 mm SL), BMNH 1847.7.21.67-69 (1: c. 147 mm SL); *Halidesmus scapularis*, BMNH 1933.10.31.1-4 (1: c. 114 mm SL); *Haliophis guttatus*, BMNH 1951.1.16.606-608 (1: c. 82 mm SL). PSEUDOCHROMINAE: *Assiculoides desmonotus*, WAM P.30929-008 (2 paratypes: 41.3–46.2 mm SL); *Assiculus punctatus*, AMS I.13113 (1: 63.0 mm SL), NTM S.10016-009 (4: 21.7–51.9 mm SL).

Subfamily Pseudoplesiopinae

Pseudoplesiopini Bleeker, 1875: 4.

Diagnosis. Members of the subfamily are diagnosed by the following synapomorphies: single tubed lateral-line scale (character 1); posterior part of pelvic bone with triangular or hook-shaped lateral process for attachment of slip of hypaxial musculature (character 2); base of anterior process on pelvic bone posteriorly positioned (character 3); coracoid articulates ventrally with medial face of lateral lamina of cleithrum (character 4); basihyal bound to anterior face of basibranchial 1 (character 5); urohyal with prominent dorsally directed process (character 6). Two additional characters provide equivocal support for monophyly of the subfamily: dorsal profile of anterior ceratohyal straight, without excavation (remnant of beryciform foramen, sensu McAllister, 1968); and all medial radials of dorsal- and anal-fin pterygiophores fused to proximal radials. Both characters also occur in the Congrogadinae, but not in the Anisochrominae, their sister group. Therefore, they may be independent autapomorphies of the Congrogadinae and Pseudoplesiopinae, or they may be synapomorphies of the more inclusive Anisochrominae + Congrogadinae + Pseudoplesiopinae clade that have undergone "reversal" in the Anisochrominae. These two characters will be discussed in greater detail in a forthcoming paper on pseudochromid intrarelationships and biogeography by the first author.

Diagnoses of pseudoplesiopine genera

Lubbockichthys n.gen.

Figs. 1, 9A, 10A, 12A, 13A, 14A

Type species. *Pseudoplesiops multisquamatus* Allen, 1987.

Diagnosis. *Lubbockichthys* is distinguished from other pseudoplesiopines by the following four autapomorphies: parietal enclosing dorsal part of supratemporal laterosensory canal (character 7; also occurs homoplastically in *Pseudoplesiops howensis*); scales cycloid at all stages of ontogeny (character 8); scales small, scales in lateral series 51–66 (character 9); and some head bones with weakly honeycombed surface (character 10). Two other characters provide equivocal support for monophyly of the genus (see

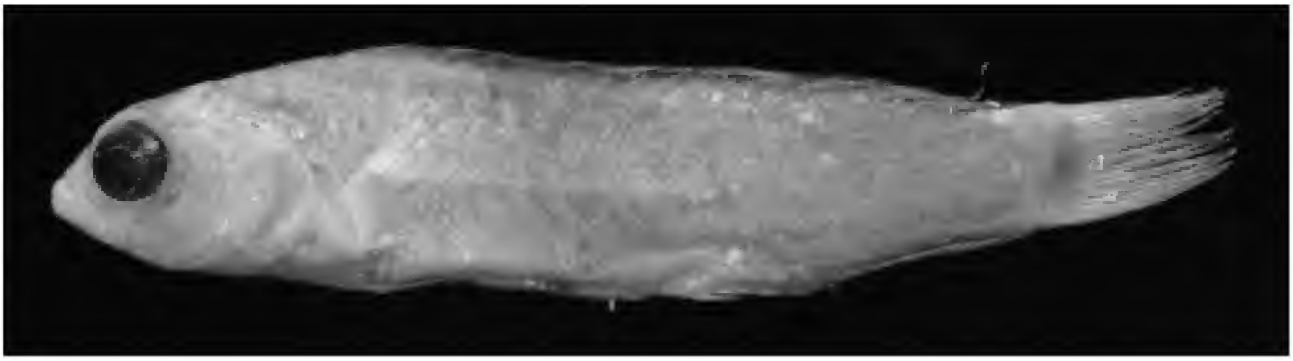


Figure 1. *Lubbockichthys multisquamatus*, WAM P.27470-002, 41.7 mm SL, holotype, Escape Reef, Great Barrier Reef.

Results of Parsimony Analysis below). The first of these, posterior interorbital pore present (character 23, state 0), is either an autapomorphy of *Lubbockichthys*, or diagnoses (state 1) a clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops*. The second character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious optimisations on the proposed phylogeny, one of which optimises mostly branched rays as an autapomorphy of *Lubbockichthys* (and homoplastically of *Pectinochromis*). Other characters useful in identifying *Lubbockichthys* are summarised in Table 2.

Included nominal species. *Pseudoplesiops multisquamatus* Allen, 1987.

Geographic distribution. Eastern Indian Ocean to the central Pacific, from the Cocos-Keeling Islands, east to the Line Islands, south to New Caledonia and north to the Ryukyu Islands.

Justification for erection of new genus. Erection of *Lubbockichthys* is justified because it establishes a monophyletic classification; species assigned to *Lubbockichthys* cannot be assigned to any other pseudoplesiopine genus without rendering that genus para- or polyphyletic. The erection of *Lubbockichthys* also draws attention to the morphological distinctiveness of the genus (and thus acknowledges a morphological gap).

Etymology. Named for the late Dr Hugh Roger Lubbock, in combination with the Greek *ichthys*, meaning fish, in recognition of Dr Lubbock's contributions to the systematics of pseudochromid fishes. Gender is masculine.

Pseudoplesiops Bleeker

Figs. 2, 9B, 10B, 11B, 12B, 13B, 14B

Pseudoplesiops Bleeker, 1858: 215 (type species, *Pseudoplesiops typus* Bleeker, by monotypy).

Nematochromis Weber, 1913: 264 (type species, *Nematochromis annae* Weber, by monotypy).

Diagnosis. *Pseudoplesiops* is demonstrably monophyletic in having the medial laminae of the pelvic bones expanded dorsally (character 11). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Nematochromis annae* Weber, 1913; *Pseudoplesiops collare* Gill, Randall & Edwards, 1991; *P. howensis* Allen, 1987; *P. revellei* Schultz, 1953; *P.*

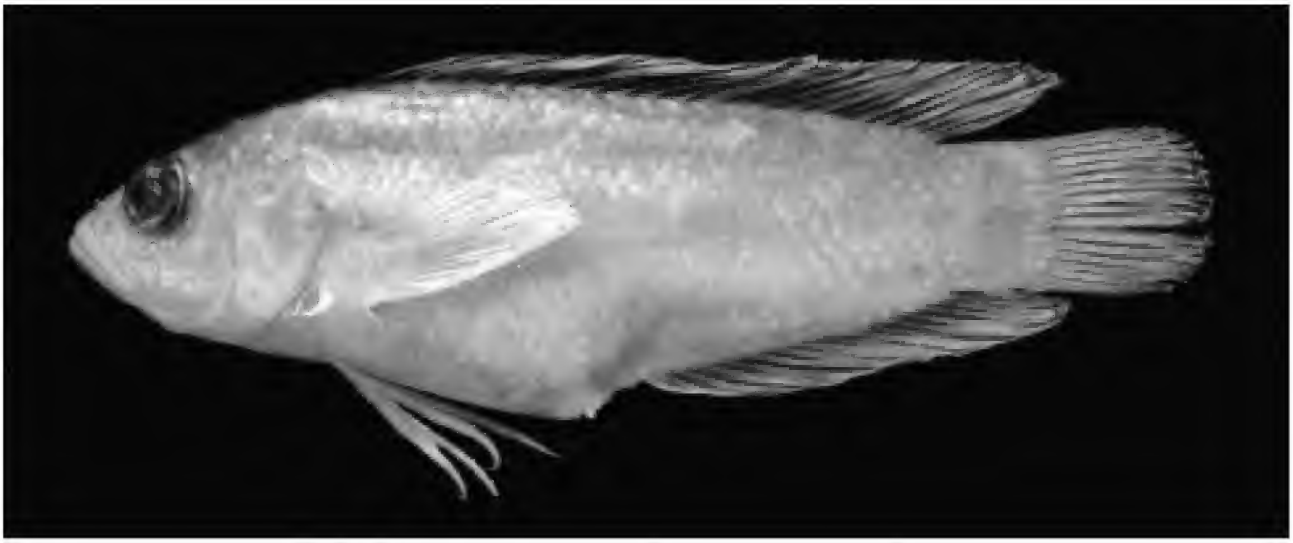


Figure 2. *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL, Ashmore Reef, Timor Sea.

rosae Schultz, 1943; *P. sargenti* Schultz, 1953; *P. typus* Bleeker, 1858.

Geographic distribution. Central Indian Ocean to the central Pacific, from the Maldive Islands, east to Oeno Atoll, north to the Ryukyu Islands and south to Lord Howe Island.

Etymology. From the Greek *pseudos*, false, and *Plesiops*, a genus of plesiopid fish, alluding to the purported similarity between the type species, *P. typus*, and *Plesiops*. Gender is masculine.

Amsichthys n.gen.

Figs. 3, 9C, 10C, 11A, 12C, 13C, 14C

Type species. *Pseudoplesiops knighti* Allen, 1987.

Diagnosis. *Amsichthys* is demonstrably monophyletic in lacking the upper preopercular pore (character 12). Monophyly of the genus is also supported by a single homoplastic character that also occurs in *Pectinochromis*: eyes large (character 30; see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops knighti* Allen, 1987.

Geographic distribution. Eastern Indian Ocean and West Pacific, from the west coast of Thailand, east to the Solomon Islands, south to the Great Barrier Reef and north to the Ryukyu Islands.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Amsichthys* as the sister group of *Pseudoplesiops*. Thus, it could be included within *Pseudoplesiops* without affecting the monophyletic status of that genus. However, we believe that character evidence for a sister relationship between the two genera is weak; such a relationship is supported by a single character, third supraneural bone well developed (character 25, state 1), but this varies among *Pseudoplesiops* species and intraspecifically in a *Chlidichthys* species (see *Results of Parsimony Analysis*). It is possible that additional characters might lead to a different phylogenetic position for *Amsichthys*; indeed, a different interpretation of characters 12 and 28, such that the reduction in number of preopercular pores was seen as homologous, would lead to *Chlidichthys* + *Pectinochromis* forming the sister of *Amsichthys*. We therefore believe that the erection of *Amsichthys* will ultimately lead to greater nomenclatural stability, as its placement as the sister to any other pseudoplesiopine genus or clade of genera will not affect the generic assignment of its constituent species.

Erection of *Amsichthys* is also partly justified on the basis of its morphological distinctiveness.

Etymology. The generic name is a combination of AMS, the standard institutional code in ichthyology for the Australian Museum, Sydney, and the Greek *ichthys*, fish. It acknowledges the generous help, encouragement and friendship given by staff of the Australian Museum's Ichthyology Section to the first author during this study and throughout his career and training. Gender is masculine.

Chlidichthys Smith

Figs. 4, 6B, 7B, 8B, 9D, 10D, 12D, 13D, 14D

Chlidichthys Smith, 1953: 518 (type species: *Chlidichthys johnvoelckeri* Smith, 1953, by monotypy).

Wamizichthys Smith, 1954: 205 (type species: *Wamizichthys bibulus* Smith, 1954, by original designation and monotypy).

Diagnosis. *Chlidichthys* is distinguished from other pseudoplesiopines and demonstrably monophyletic in having two autapomorphies: lower lip interrupted at symphysis (character 13); and second infraorbital bone absent (character 26, state 2). Two other characters, 31 (state 0; mostly unbranched dorsal-fin rays) and 32 (state 1; mostly unbranched anal-fin rays), provide equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Chlidichthys abruptus* Lubbock, 1977; *C. auratus* Lubbock, 1975; *Wamizichthys bibulus* Smith, 1954; *C. cacatuoides* Gill & Randall, 1994; *C. inornatus* Lubbock, 1976; *C. johnvoelckeri* Smith, 1953;

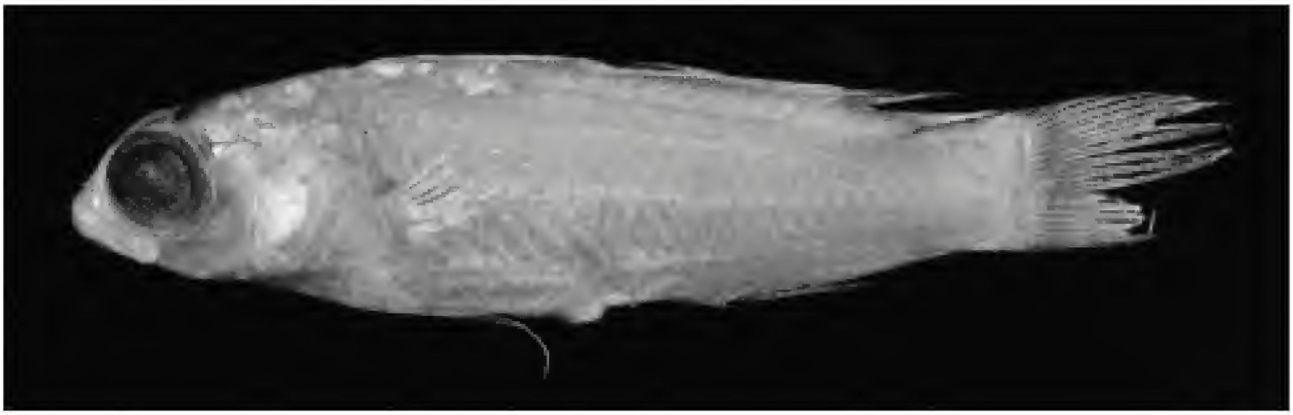


Figure 3. *Amsichthys knighti*, NTM S.11384-018, North Reef, Timor Sea.

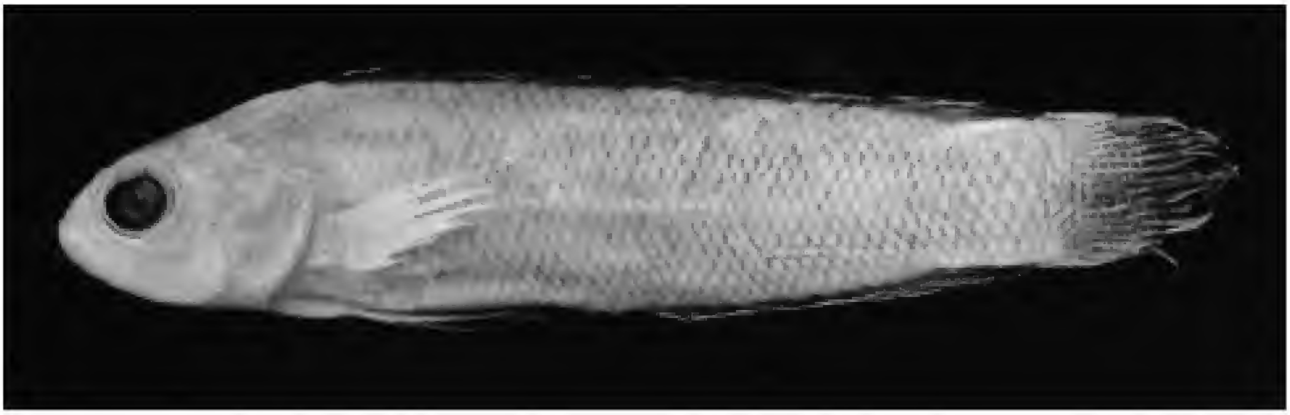


Figure 4. *Chlidichthys johnvoelckeri*, CAS 35451, 45.7 mm SL, Grande Comore Island, Comoro Islands.

C. pembae Smith, 1954; *C. randalli* Lubbock, 1977; *C. rubiceps* Lubbock, 1975; *C. smithae* Lubbock, 1977.

Geographic distribution. Western Indian Ocean, from the northern Red Sea and east Africa, north to southern Oman, east to Sri Lanka and south to Natal, South Africa.

Etymology. Apparently from the Greek *chlidanos*, delicate or luxurious, and *ichthys*, fish. Gender is masculine.

Pectinochromis n.gen.

Figs. 5, 9E, 10E, 12E, 13E, 14E

Type species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Diagnosis. *Pectinochromis* is distinguished from other pseudoplesiopine genera and demonstrably monophyletic in having six autapomorphies: first dorsal-fin pterygiophore expanded anteriorly (character 14); first dorsal-fin pterygiophore with lateral processes (character 15); second pterygiophore of dorsal fin inserts between neural spines 3 and 4 (character 16); dorsal fin anteriorly positioned (character 17); single supraneural bone (character 18); gill rakers relatively numerous (character 19). Monophyly of the genus is also supported by a single homoplastic character, eyes large (character 30), that also occurs in *Amsichthys*. Another homoplastic character, dorsal-fin rays mostly branched (character 31, state 1), has three equally parsimonious character optimisations within the Pseudoplesiopinae; two of the optimisations identify it as an autapomorphy of *Pectinochromis*. The presence of mostly branched anal-fin rays (character 32) also provides equivocal support for monophyly of the genus (see *Results of Parsimony Analysis* below for discussion of this and the previous two characters). Other characters useful in identifying the genus are summarised in Table 2.

Included nominal species. *Pseudoplesiops lubbocki* Edwards & Randall, 1983.

Geographic distribution. Red Sea.

Justification for erection of new genus. Our current hypothesis of generic relationships of pseudoplesiopines places *Pectinochromis* as the sister group of *Chlidichthys*; this relationship is strongly supported by five synapomorphies (see *Results of Parsimony Analysis* below). Thus, *Pectinochromis* could be included within *Chlidichthys* without affecting the monophyletic status of that genus. However, our decision to erect *Pectinochromis* is to draw attention to the morphological distinctiveness of the two genera. *Pectinochromis* is particularly distinctive, and is readily distinguished from all other pseudochromids by its unusual dorsal-fin and gill-raker morphology.

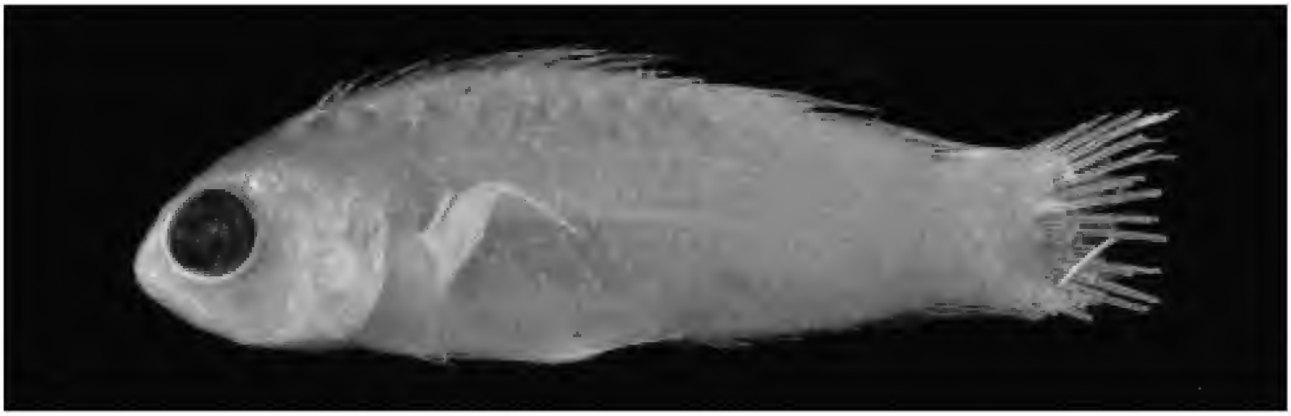


Figure 5. *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL, Gulf of Aqaba, Red Sea.

Table 1. Matrix of 32 characters of pseudoplesiopine genera (see text for details of characters).

	character number						
		1		2		3	
	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2
outgroup	0 0 0 0 0	0 0 0 0 0	? 0 0 0 0	0 0 0 0 0	0 0 ? 0 0	0 0 0 0 0	? 0
Lubbockichthys	1 1 1 1 1	1 1 1 1 1	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	1 0
Pseudoplesiops	1 1 1 1 1	1 0 0 0 0	1 0 0 0 0	0 0 0 0 1	1 1 1 1 0	0 0 0 0 0	0 1
Amsichthys	1 1 1 1 1	1 0 0 0 0	0 1 0 0 0	0 0 0 0 1	1 1 1 1 0	0 0 0 0 1	0 1
Chlidichthys	1 1 1 1 1	1 0 0 0 0	0 0 1 0 0	0 0 0 0 1	1 1 1 0 1	2 1 1 1 0	0 1
Pectinochromis	1 1 1 1 1	1 0 0 0 0	0 0 0 1 1	1 1 1 1 1	1 1 1 0 1	1 1 1 1 1	1 0

Etymology. The generic name is from the Latin *pecten*, a comb or rake, and the Greek *Chromis*, a genus of pomacentrid fish, which has been used as a suffix for various pseudochromid genera (e.g., *Pseudochromis* and *Nematochromis*), and alludes to the relatively high number of gill rakers. Gender is feminine, in keeping with the accepted gender of *Chromis* [see Opinion 1417 (International Commission on Zoological Nomenclature, 1986) for ruling on the gender of *Chromis*].

Phylogenetic relationships

Character descriptions. A summary of character state distributions is given in Table 1.

Character 1. Single tubed anterior lateral-line scale. Pseudochromines and anisochromines have a series of tubed scales in the anterior portion of the lateral line (state 0). Pseudoplesiopines usually have only a single tubed scale, which is situated near the branchial opening (state 1; occasional specimens of *Lubbockichthys* species may have two tubed scales on one or both sides of the body). Congrogadines vary somewhat in the structure of their lateral line, but most have a single, anterodorsal lateral line consisting of a series of tubed scales (exceptions are *Rusichthys*, which lacks a lateral line, *Halidesmus*, which has three lateral lines, and *Halimuraenoides*, some *Halimuraena* species, one *Haliophis* species and occasional specimens of some *Congrogadus* species, all of which have two lateral lines, one anterodorsal, the other midlateral). The state found in pseudoplesiopines is regarded as apomorphic.

Character 2. Posterior part of pelvic bone with triangular or hook-shaped lateral process. Pseudochromines, anisochromines and congrogadines lack lateral processes on the posterior part of the pelvic bone (state 0; Fig. 6A). Pseudoplesiopines have a triangular or hook-shaped lateral process on the posterior part of the pelvic bone, which serves as an attachment site for a slip of hypaxial musculature (state 1; Fig. 6B). This arrangement is regarded as apomorphic.

Character 3. Base of anterior process on pelvic bone posteriorly positioned. The base of the anterior process (sensu Stiassny & Moore, 1992) of the pelvic bone of pseudochromines and anisochromines is positioned slightly to well anterior to the anterior edge of the pelvic-fin spine base (Fig. 6A; state 0). Congrogadines examined by us lack an anterior process on the pelvic bone. In pseudoplesiopines, the anterior process is positioned noticeably posterior to the anterior edge of pelvic-fin spine base (Fig. 6B; state 1). The latter state is regarded as apomorphic.

Character 4. Coracoid articulates ventrally with medial face of lateral lamina of cleithrum. In pseudochromines, anisochromines and congrogadines the ventral process of the coracoid attaches to the lateral face of a medial lamina on the cleithrum (Fig. 7A; state 0), whereas in pseudoplesiopines the coracoid attaches to the medial face of a lateral lamina (Fig. 7B; state 1). The latter state is regarded as apomorphic.

Character 5. Basihyal bound to anterior face of basibranchial 1. The basihyal loosely overlies basibranchial 1 in pseudochromines and anisochromines (Fig. 8A,C; state 0). It is tightly bound by connective tissue to the anterior face of basibranchial 1 in pseudoplesiopines (Fig. 8B; state 1). The basihyal is bound more-or-less tightly to basibranchial 1 in congrogadines (Fig. 8D), but the arrangement does not appear to be homologous with the condition found in pseudoplesiopines. Most notably, the condition in congrogadines differs in that there are two articulation points between the two bones, a dorsal attachment between the mid-dorsal face of basibranchial 1 and the posterior tip of the basihyal, and a ventral attachment between the anterior (cartilaginous) tip of basibranchial 1 and the posteroventral edge of the basihyal. In the latter attachment, the basihyal is embraced by small lateral projections that extend anteriorly from basibranchial 1 (and obscure the anterior cartilage tip from lateral view). The congrogadine condition is associated with a very different arrangement of the basibranchial 1/urohyal articulation, where the urohyal is positioned farther posteriorly (as it is also in anisochromines), articulating with a posteroventral process from basibranchial 1 (versus weakly associated with the anterior cartilage tip of basibranchial 1 in pseudochromines and pseudoplesiopines). We consider the basihyal/basibranchial 1 arrangement displayed by pseudoplesiopines to be apomorphic within the Pseudochromidae.

Character 6. Urohyal with prominent dorsally directed process. The urohyal of pseudochromines has a small to moderately developed posterodorsally directed process, which is weakly embraced by anteroventrally projecting processes from the hypobranchials 1 (Fig. 8A; state 0).

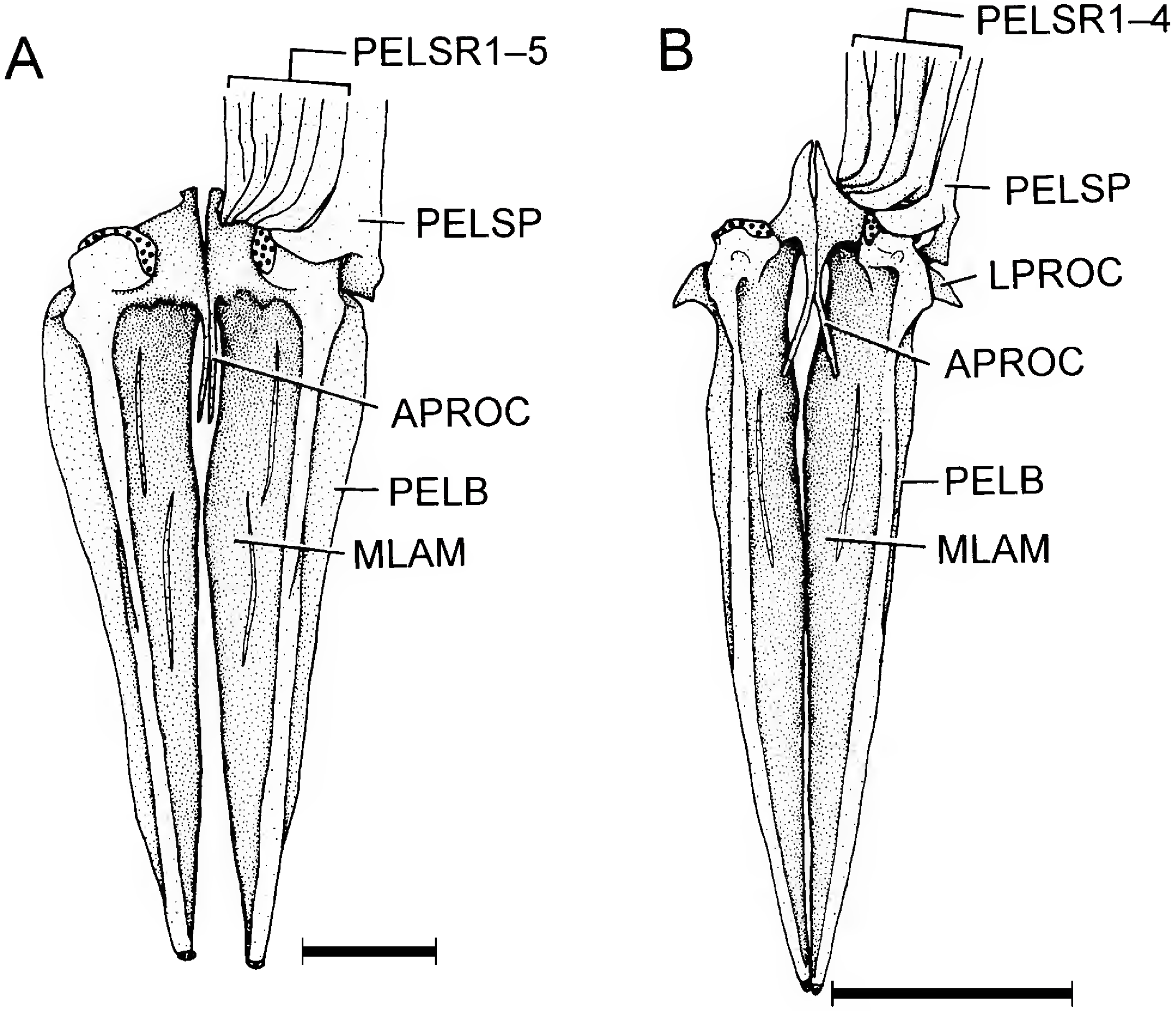


Figure 6. Pelvic girdles of two pseudochromid species in ventral view: A, "*Pseudochromis*" cf. *paccagnellae* (Pseudochrominae), AMS I.22613-008, 46.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Anterior to bottom of page; cartilage shown in large stipple. Abbreviations: APROC, anterior process; LPROC, lateral process; MLAM, medial lamina; PELB, pelvic bone; PELSP, pelvic-fin spine; PELSR1–5, pelvic segmented rays 1–5. Scale bars = 1 mm.

Pseudoplesiopines have a prominent dorsal process on the urohyal, which is also embraced by anteroventral processes from the hypobranchials 1, but it is dorsally rather than posterodorsally directed (Fig. 8B; state 1). Anisochromines and congrogadines lack a dorsal process from the urohyal to the hypobranchials 1; the urohyal is well separated from the hypobranchials, and the hypobranchials have small posteroventrally (rather than anteroventrally) projecting processes (Fig. 8C,D). The condition shown by pseudoplesiopines is considered apomorphic within the Pseudochromidae.

Character 7. Parietal bears enclosed lateral-line canal. In *Chlidichthys, Amsichthys, Pectinochromis* and most *Pseudoplesiops*, the dorsal portion of the supratemporal lateral-line commissure passes over the parietal as a membranous canal, which is either unossified or ossified medially only (Fig. 9B–E; state 0). In *Lubbockichthys* and *Pseudoplesiops howensis*, the dorsal portion of the supratemporal lateral-line commissure passes through a fully ossified (enclosed) canal in the parietal (Fig. 9A; state 1). In *Assiculoides* and *Assiculus*, the supratemporal commissure passes over the parietal in a membranous tube that is either unossified or medially ossified only; anisochromines have similar ossification of the canal, but the commissure is heavily branched and continuous across the dorsal midline. In congrogadines, the commissure is also continuous across the dorsal midline, but is mostly ossified throughout its length. As far as we can ascertain, the ossified portion is separate from, though closely applied to, the parietal bone. We therefore consider the condition shown by *Lubbockichthys* and *P. howensis* apomorphic.

Character 8. Scales "cycloid" at all stages of ontogeny. *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* have cteni on posterior body scales, at

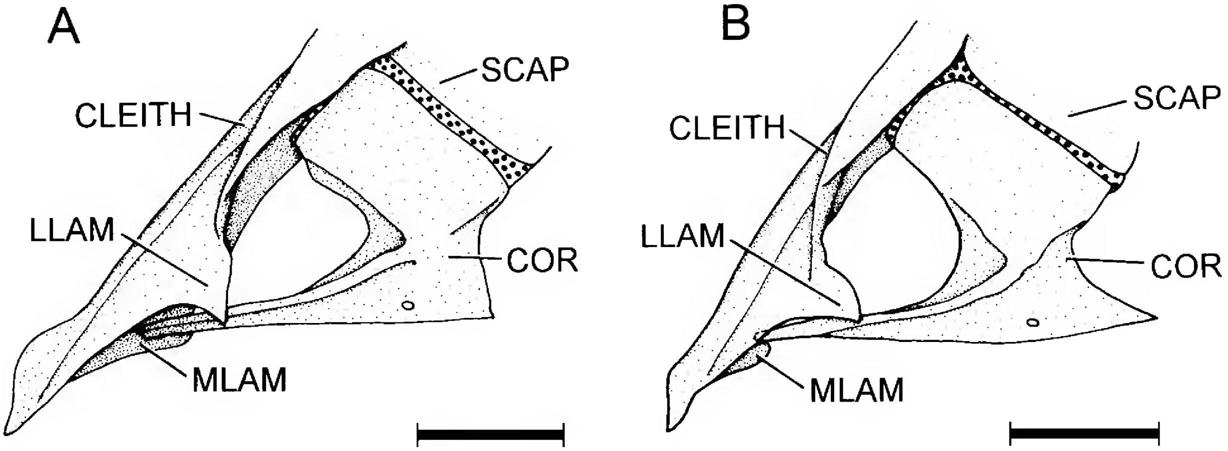


Figure 7. Right lateral view (reversed) of lower part of pectoral girdle of two pseudochromid species: A, "*Pseudochromis*" *diadema* (Pseudochrominae), USNM 210017, 35.0 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL. Abbreviations: CLEITH, cleithrum; COR, coracoid; MLAM, medial lamina of cleithrum; LLAM, lateral lamina of cleithrum; SCAP, scapula. Scale bars = 1 mm.

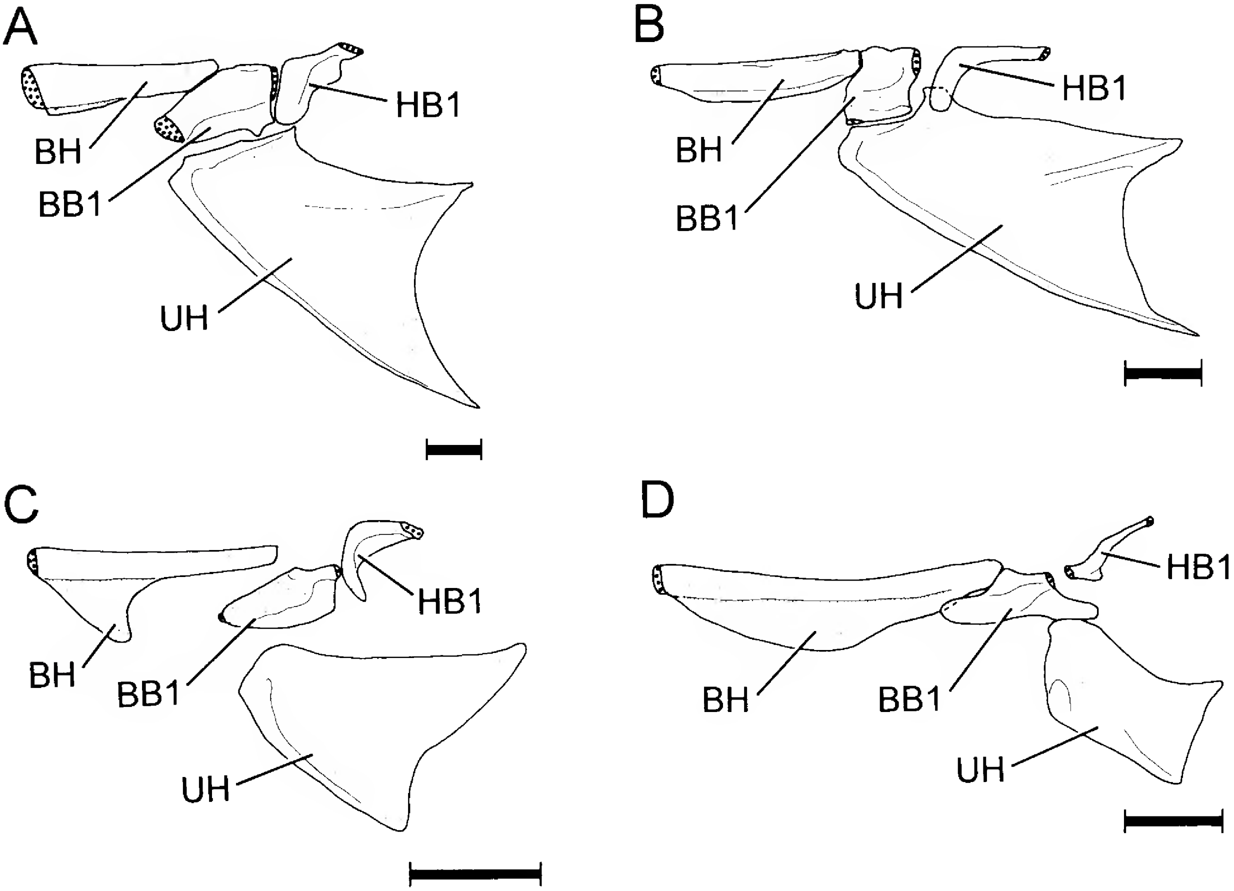


Figure 8. Right lateral view (reversed) of basihyal (BH), basibranchial 1 (BB1), hypobranchial 1 (HB1) and urohyal (UH) of selected pseudochromid species: A, *Assiculus punctatus* (Pseudochrominae), NTM S.10016-009, 32.2 mm SL; B, *Chlidichthys johnvoelckeri* (Pseudoplesiopinae), CAS 35451, 37.9 mm SL; C, *Anisochromis kenyae* (Anisochrominae), RUSI 4906, 23.3 mm SL; D, *Blennodesmus scapularis* (Congrogadinae), AMS I.26723-087, 49.7 mm SL. Cartilage shown in large stipple. Scale bars = 0.5 mm.

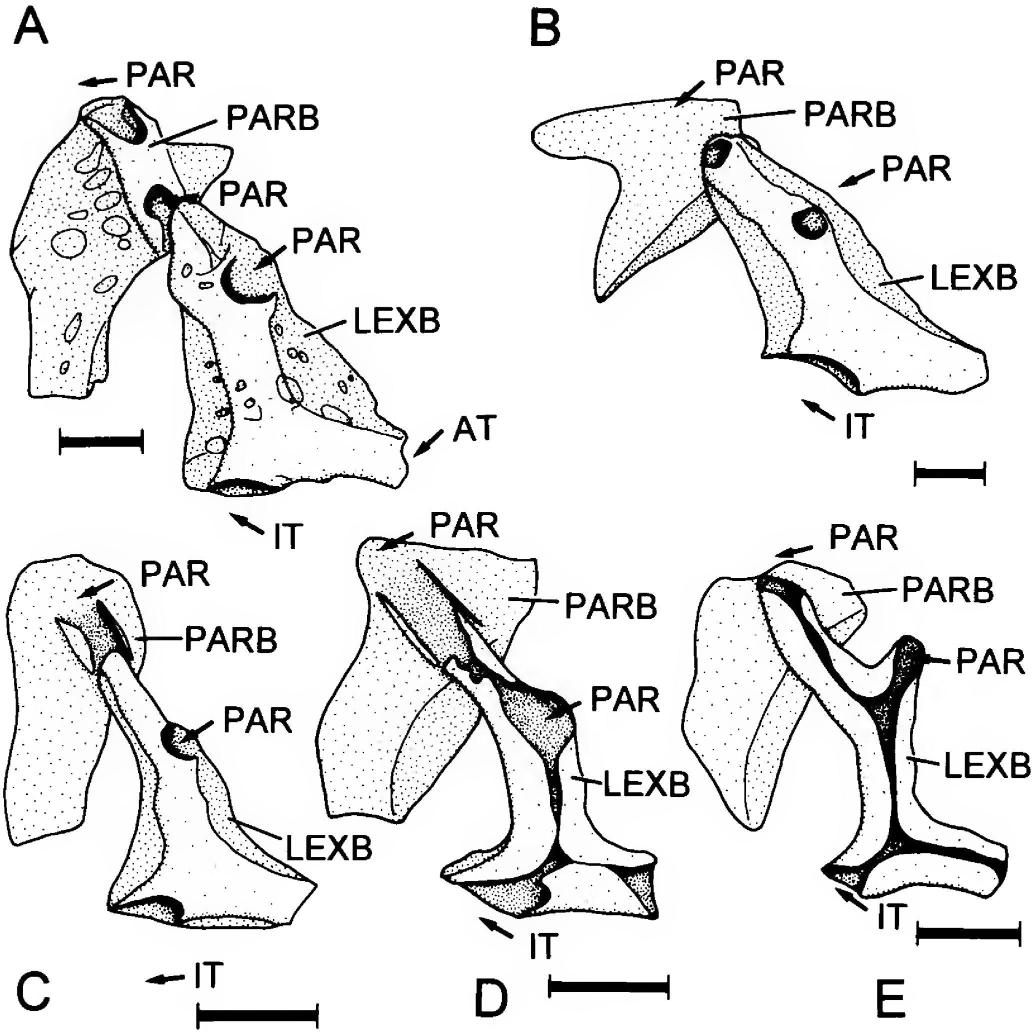


Figure 9. Lateral extrascapulae and parietal bones and associated laterosensory pores of selected pseudoplesiopine species: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate locations of sensory pores. Abbreviations: AT, anterior temporal pore; IT, intertemporal pore; LEXB, lateral extrascapular bone; PAR, parietal pore; PARB, parietal bone. Scale bars = 0.5 mm.

least as juveniles (state 0), as do pseudochromines and anisochromines and the vast majority of perciforms. Species of *Lubbockichthys* are unique among pseudoplesiopines in lacking cteni on body scales at all stages of ontogeny (state 1). The posterior body scales of congrogadines also lack cteni, as do those of some perciform taxa, such as ambassids, bathyclupeids, carangoids, cepolids, dinolestids, lactariids, leiognathids, opistognathids, sinipercids, clinids, dactyloscopids, zoarcoids, and most cirrhitoids (see Johnson, 1984: table 120; Roberts, 1993: appendix 1). Such scales have been generally termed "cycloid", but they are not homologous with the cycloid scales of lower teleosts (J. Radding, pers. comm.). Cteni are present in small (less than about 30 mm SL) specimens of *Pseudoplesiops typus*, but are absent from larger specimens; presumably cteni are either shed or, more likely, resorbed with growth. Other species of *Pseudoplesiops* retain cteni on posterior body scales throughout ontogeny. We regard the condition found in *Lubbockichthys* as apomorphic and nonhomologous with that found in *P. typus*.

Character 9. Scales small. Chlidichthys, Amsichthys, Pectinochromis and *Pseudoplesiops* have relatively large to moderately small scales (state 0). In contrast, *Lubbockichthys* has relatively small scales (state 1). This character can be seen by differences in numbers of scales in lateral series (Table 2): 37–52 in *Chlidichthys*, 30–33 in *Amsichthys*, 35–39 in *Pectinochromis* and 26–42 in *Pseudoplesiops*, versus 51–66 in *Lubbockichthys*. Most of the outgroup taxa have relatively large to moderately small scales. Scales in lateral series counts range from 39–44 in anisochromines, 35–42 in *Assiculoides*, and 38–46 in *Assiculus*. However, congrogadines also have numerous, small scales. Nevertheless,

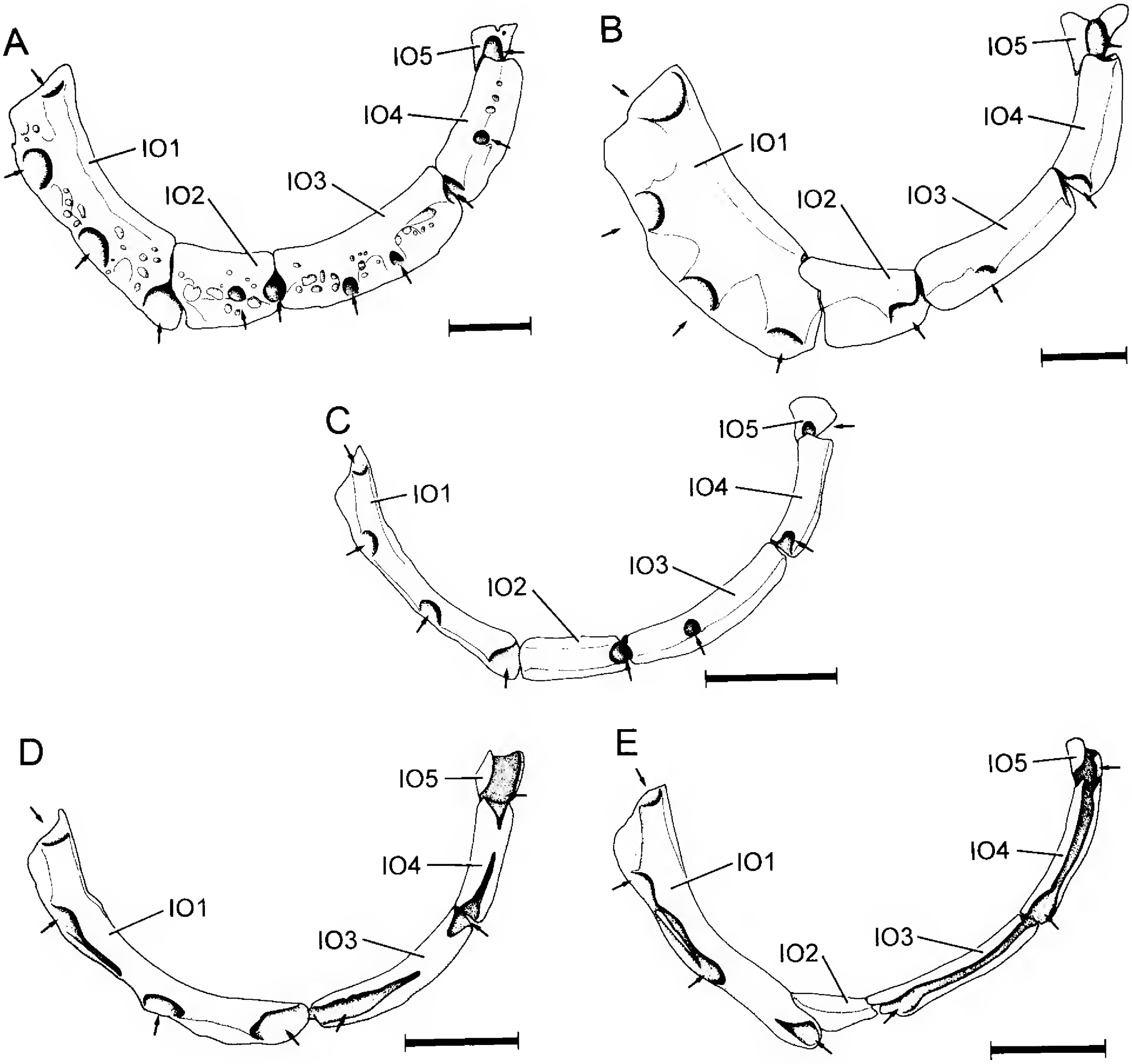


Figure 10. Infraorbital bones (IO1-5) of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, ROM CS585, 49.0 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Arrows indicate positions of suborbital pores. Scale bars = 1 mm.

the condition shown by *Lubbockichthys* is most parsimoniously argued to be derived within the Pseudoplesiopinae.

Character 10. Some head bones with weakly honeycombed surface. Pseudoplesiops, Amsichthys, Pectinochromis and *Chlidichthys* have relatively smooth head bones (e.g., Figs. 9B–E, 10B–E; state 0), as do the outgroup taxa. *Lubbockichthys* has at least some head bones with a weakly honeycombed surface (e.g., Figs. 9A, 10A; state 1). We consider this condition to be apomorphic within the Pseudoplesiopinae.

Character 11. Medial laminae of pelvic bones expanded dorsally. The medial laminae (= inner wing of Stiassny & Moore, 1992) of the pelvic bones of *Lubbockichthys, Amsichthys, Chlidichthys* and *Pectinochromis* are at most weakly expanded dorsally, so that the pelvic bones have a concave to weakly convex dorsal profile (Fig. 11A; state 0). The medial laminae of the pelvic bones of *Pseudoplesiops* are strongly expanded dorsally, so that the bones have a strongly convex dorsal profile (Fig. 11B; state 1). Anisochromines and the basal congrogadine genus *Rusichthys* have dorsally expanded medial laminae (with the exception of *Halidesmus scapularis*, more derived congrogadine genera lack dorsally expanded medial laminae, but this appears to be associated with reduction or loss of the pelvic fin), whereas *Assiculoides* and *Assiculus* (and all other pseudochromines) have weakly expanded laminae on the pelvic bones. Because both states occur in the outgroup taxa, this character was not polarised.

Character 12. Loss of uppermost preopercular pore. Lubbockichthys, Pseudoplesiops, Pectinochromis and *Chlidichthys* and the outgroup taxa have the uppermost preopercular pore associated with the terminal opening in the preopercle (Fig. 12A,B,D,E; state 0). *Amsichthys* is distinctive in usually lacking a pore at the dorsal terminus of the preopercle (Fig. 12C; state 1). We consider the absence of the dorsal pore apomorphic. A terminal pore was present on one or both sides of the head of a few, relatively large specimens of *Amsichthys*; in contrast, a terminal pore was consistently present in juveniles and adults of the other pseudoplesiopine genera and in the outgroups. This suggests that the pore may develop relatively late in ontogeny in *Amsichthys*, in which case the character should be redescribed as delayed development of uppermost preopercular pore rather than loss of uppermost preopercular pore.

Character 13. Lower lip interrupted at symphysis. Amsichthys, Lubbockichthys, Pectinochromis, Pseudoplesiops, anisochromines, congrogadines, *Assiculoides* and *Assiculus* have the lower lip uninterrupted at the symphysis (Gill & Randall, 1994: fig. 1A; Gill & Hutchins, 1997: fig. 4; state 0). *Chlidichthys* species are unique among pseudoplesiopines in having the lower lip interrupted at the symphysis (Gill & Randall, 1994: fig. 1B; state 1). We consider the latter condition apomorphic.

Character 14. First dorsal-fin pterygiophore expanded anteriorly. The anterior face of the first dorsal-fin pterygiophore is at best weakly expanded anteriorly in *Chlidichthys, Amsichthys, Lubbockichthys* and *Pseudoplesiops* (Fig. 13A–D; state 0). *Pectinochromis* is unusual in having the anterior part of the first dorsal-fin pterygiophore strongly expanded anteriorly (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* have the anterior face of the first pterygiophore weakly expanded anteriorly; congrogadines lack the homologue of the first dorsal-fin pterygiophore (Gill, 1998). We therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 15. First dorsal-fin pterygiophore with lateral processes. Chlidichthys, Amsichthys, Lubbockichthys and *Pseudoplesiops* lack lateral processes on the first dorsal-fin pterygiophore (Fig. 13A–D; state 0). *Pectinochromis* is distinctive in having prominent lateral processes on the first dorsal-fin pterygiophore (Fig. 13E; state 1). Anisochromines, *Assiculoides* and *Assiculus* lack such processes (and, as noted above, congrogadines lack the homologue of the first pterygiophore), and we therefore consider the condition shown by *Pectinochromis* apomorphic.

Character 16. Second dorsal-fin pterygiophore insertion between neural spines 2 and 3. Chlidichthys, Amsichthys, Lubbockichthys, Pseudoplesiops, anisochromines, *Assiculus* and *Assiculoides* have the first dorsal-fin pterygiophore insertion between neural spines 2 and 3, and the next two pterygiophores between neural spines 3 and 4 (Fig. 13A–D; state 0). Congrogadines have only two dorsal-fin pterygiophores inserting anterior to neural spine 4, both positioned between neural spines 3 and 4, owing to the loss of the first pterygiophore (Gill, 1998). *Pectinochromis* has the first two pterygiophores between neural spines 2 and 3, and the third pterygiophore between neural spines 3 and 4 (Fig. 13E; state 1). The anterior position of the second pterygiophore is regarded as apomorphic.

Character 17. Dorsal fin anteriorly positioned. The dorsal-fin origin of *Lubbockichthys, Pseudoplesiops, Amsichthys* and *Chlidichthys* is near the vertical through the posterior edge of the operculum (Figs. 1–4, 12A–D; state 0), as it is in the outgroup taxa. *Pectinochromis* is unusual in having the dorsal-

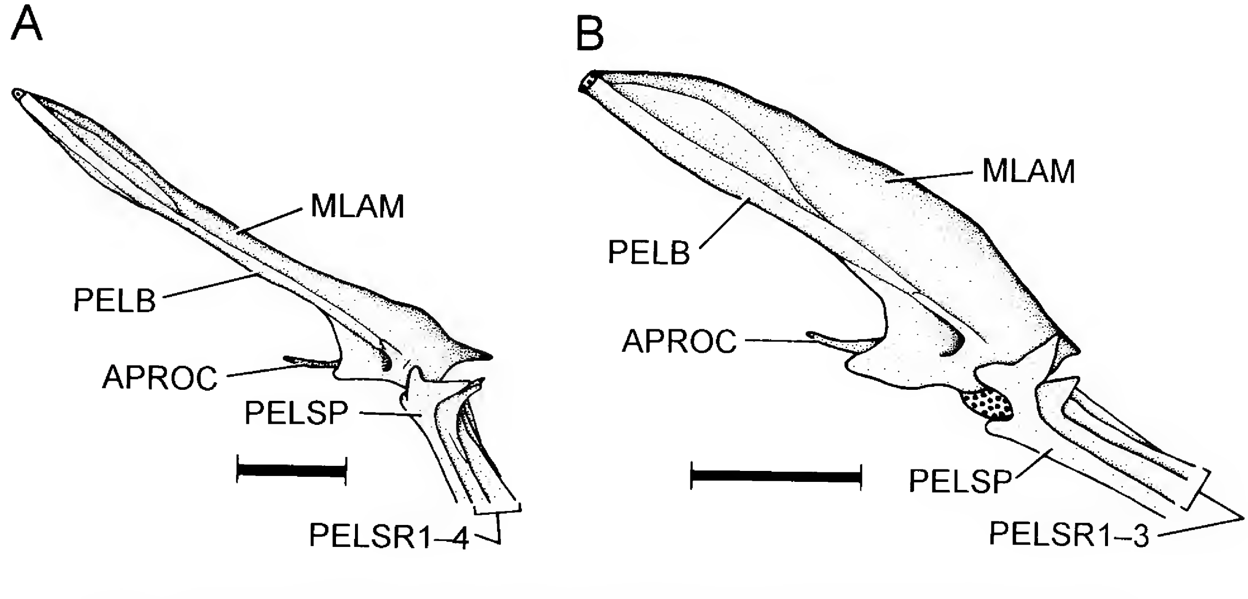


Figure 11. Right lateral view (reversed) of pelvic girdles of two pseudoplesiopine species: A, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; B, *Pseudoplesiops rosae*, AMS I.22582-073, 22.0 mm SL. Abbreviations as in Fig. 1. Cartilage shown in large stipple. Scale bars = 0.5 mm.

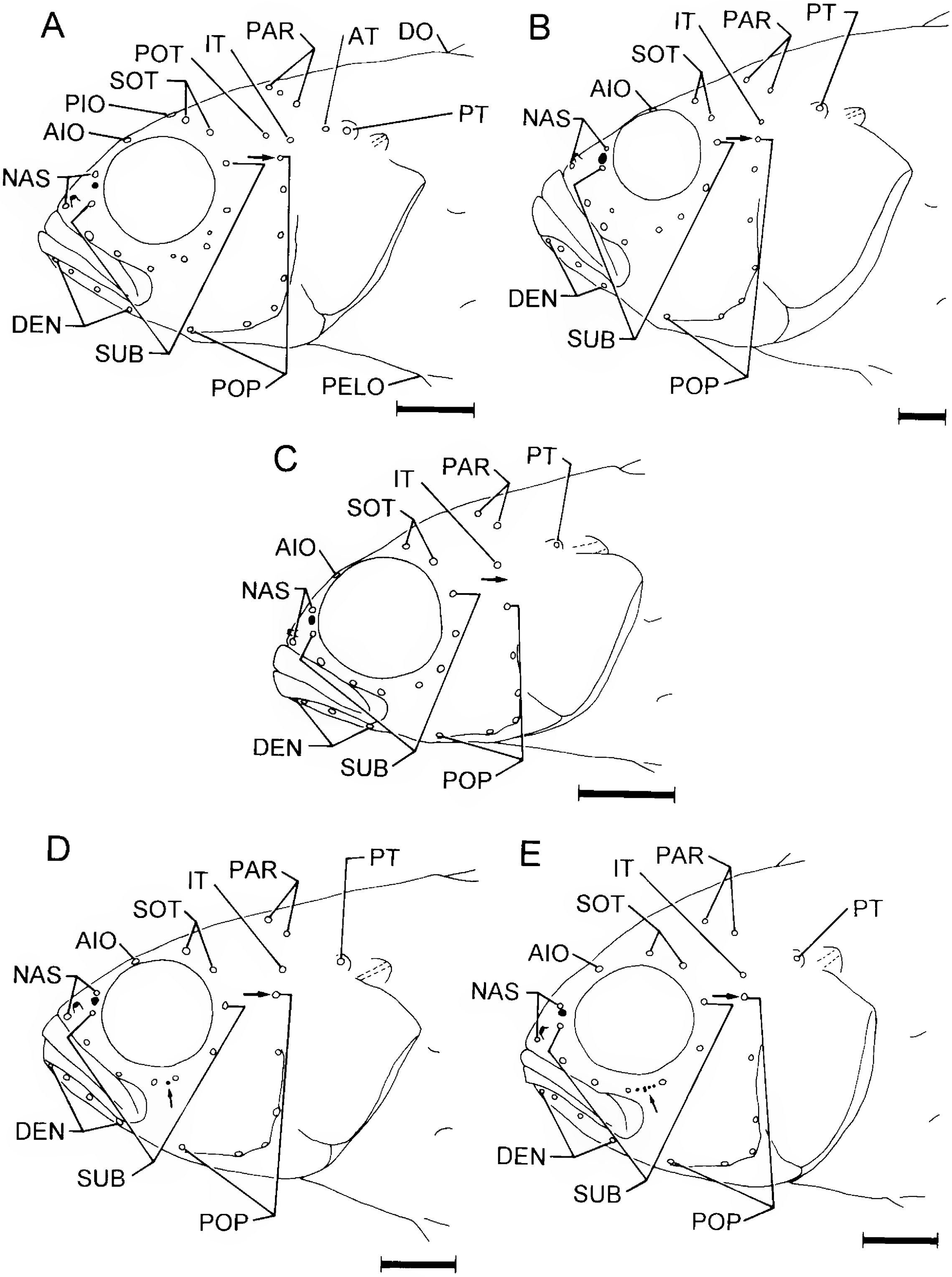


Figure 12. Left lateral diagrams of heads of selected pseudoplesiopine species: A, *Lubbockichthys multisquamatus*, AMS I.220779-175, 36.3 mm SL; B, *Pseudoplesiops typus*, WAM P.30842-019, 54.6 mm SL; C, *Amsichthys knighti*, NTM S.11384-018, 25.0 mm SL; D, *Chlidichthys johnvoelckeri*, ROM uncat., (field number RW 88-26), 36.2 mm SL; E, *Pectinochromis lubbocki*, BMNH 1982.6.9.1-4, 32.2 mm SL (paratype). Large arrow indicates dorsal tip of preopercle. Superficial neuromasts in D and E shown in black and indicated by small arrow. Abbreviations: AIO, anterior interorbital pore; AT, anterior temporal pore; DEN, dentary pores; DO, dorsal-fin origin; IT, intertemporal pore; NA, nasal pores; PLO, pelvic-fin origin; PAR, parietal pores; PIO, posterior interorbital pore; POP, preopercular pores; POT, posterior otic pore; PT, posttemporal pore; SOB, suborbital pores; SOT, supraotic pores. Scale bars = 2 mm.

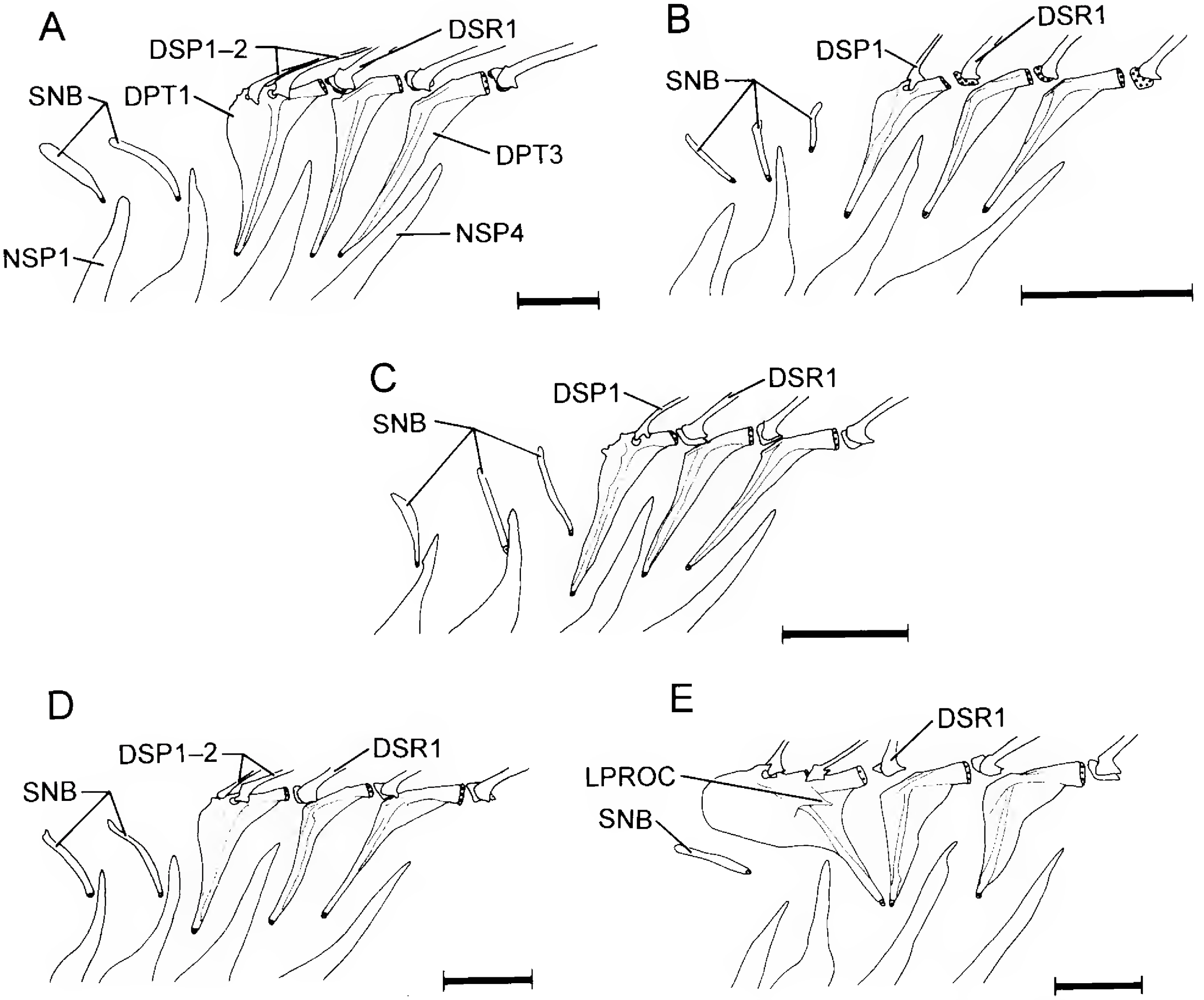


Figure 13. Anterior dorsal-fin pterygiophores and supraneural bones of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops howensis*, AMS I.19755-024, 21.0 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in large stipple. Abbreviations: DPT1,3, dorsal-fin pterygiophores 1,3; DSP1-2, dorsal-fin spines 1–2; DSR1, segmented dorsal-fin ray 1; LPROC, lateral process on first dorsal-fin pterygiophore; NSP1,4, neural spines 1,4; SNB, supraneural bones. Scale bars = 1 mm.

fin origin near the vertical through the preopercle (Figs. 5, 7E; state 1), a condition that we consider apomorphic.

Character 18. Single supraneural bone. Lubbockichthys, Pseudoplesiops, Amsichthys, Chlidichthys, Assiculoides, Assiculus and anisochromines have more than one supraneural bone (Fig. 13A–D; state 0). *Pectinochromis* has a single supraneural bone (Fig. 13E; state 1). Congrogadines have one to three tiny supraneural bones, varying considerably within species. We regard the single supraneural in *Pectinochromis* apomorphic.

Character 19. Numerous outer first-gill-arch rakers. Most pseudoplesiopines have relatively low to moderate numbers of total rakers on the outer face of the first gill arch: 12–16 for *Amsichthys*; 9–17 for *Pseudoplesiops*; 12–19 for *Chlidichthys*; and 12–21 for *Lubbockichthys* (state 0). The outgroup taxa have similar low to moderate numbers: 3–9 in anisochromines; 6–17 in congrogadines; 14–18 in *Assiculoides*; and 13–17 in *Assiculus*. *Pectinochromis* is distinctive in having numerous rakers on the outer face of the first arch, ranging from 27–31 (state 1). This state is regarded as apomorphic.

Character 20. Segmented pelvic-fin rays all unbranched. Adult specimens of *Lubbockichthys* have one or more segmented pelvic-fin rays branched (state 0). *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* have all segmented pelvic-fin rays unbranched, (state 1). With the exception of some congrogadines that lack pelvic fins, the outgroup taxa have one or more branched segmented rays in the pelvic fin. The absence of branched rays is therefore regarded as apomorphic.

Character 21. Posterior otic pores absent. Adult specimens of *Lubbockichthys* have one or more posterior otic pores on each side of the head (Fig. 12A; state 0). The remaining pseudoplesiopine genera lack posterior otic pores (Fig. 12B–E; state 1). Posterior otic pores are present in *Assiculus, Assiculoides* and anisochromines, and are either present (*Halidesmus, Halimuraenoides* and *Congrogadus* (*Congrogadus*)) or absent (*Rusichthys, Haliophis, Natalichthys, Blennodesmus, Halimuraena* and *Congrogadus* (*Congrogadoides*)) in congrogadines (Winterbottom, 1986, 1996; Winterbottom & Randall, 1994). The lack of posterior otic pores is regarded as apomorphic within the Pseudoplesiopinae.

Character 22. Anterior temporal pores absent. Adult specimens of *Lubbockichthys* have an anterior temporal pore on each side of the head (Figs. 9A, 12A; state 0). The remaining pseudoplesiopine genera lack anterior temporal pores (Figs. 9B–E, 12B–E; state 1). *Assiculus, Assiculoides*, anisochromines and congrogadines possess anterior temporal pores; the absence of anterior temporal pores is therefore apomorphic within the Pseudoplesiopinae.

Character 23. Posterior interorbital pores. Adult specimens of *Lubbockichthys* have 1–2 (usually 1) median posterior interorbital pores on the head (Fig. 12A; state 0). The remaining pseudoplesiopine genera lack median posterior interorbital pores (Fig. 12B–E; state 1). *Assiculoides* and *Assiculus* lack median posterior interorbital pores. However, such pores are present in anisochromines and the majority of congrogadines. The polarity of this character within the Pseudoplesiopinae is, therefore, equivocal.

Character 24. Third supraneural bone well developed. The third supraneural bone is small or absent in *Lubbockichthys, Pectinochromis*, anisochromines, congrogadines, *Assiculoides, Assiculus* and all but one species of *Chlidichthys* (Fig. 13A,D,E; state 0). *Amsichthys* and all but a few relatively derived *Pseudoplesiops* species have the third supraneural bone well developed (Fig. 13B,C; state 1), a condition that we consider to be apomorphic. *Chlidichthys abruptus* is unique among pseudoplesiopines in exhibiting considerable intraspecific variation in this character; approximately one quarter of specimens examined lacked a third supraneural bone, whereas the remaining specimens had a weakly to well-developed third supraneural bone.

Character 25. Three epurals. Lubbockichthys, Amsichthys and *Pseudoplesiops* have two epurals (Fig. 14A–C; state 0), as do anisochromines, *Assiculoides* and basal congrogadines. *Chlidichthys* and *Pectinochromis* have three epurals (Fig. 14D,E; state 1). *Assiculus* and most of the remaining pseudochromines also have three epurals. [The exceptions, aside from *Assiculoides*, are members of the *Pseudochromis tapeinosoma* group (Gill & Allen, 1996), which have two epurals.] Taken in the context of the scheme of outgroup relationships proposed herein, the three-epural state is most parsimoniously interpreted as apomorphic among pseudoplesiopines.

Character 26. Infraorbital 2 reduced or absent. In *Lubbockichthys, Amsichthys* and *Pseudoplesiops*, the infraorbital branch of the cephalic lateral-line systems passes through an uninterrupted series of canals in the five infraorbital bones (Fig. 10A–C; state 0). In *Pectinochromis*, infraorbital 2 is reduced in size and lacks a lateral-line canal, so that the canal passing through infraorbital 1 (lachrymal) does not communicate with the posterior series of canals (Fig. 10E; state 1). Infraorbital 2 is absent in *Chlidichthys*, giving a total of only four infraorbitals, and the canal passing through infraorbital 1 usually (see below) does not communicate with the posterior series of canals (Fig. 10D; state 2). The only *Chlidichthys* species in which there is communication between the anterior and posterior portions of the infraorbital canal (i.e., between infraorbitals 1 and 3) are the three members of a derived clade within the genus, *C. cacatuoides, C. inornatus* and *C. rubiceps*; we consider the uninterrupted series of infraorbitals in these species secondarily derived, and non-homologous with the outgroup condition. The outgroup taxa usually have the infraorbital branch of the cephalic lateral-line system passing through an uninterrupted series of canals in four (congrogadine genus *Natalichthys*), five (*Assiculoides*, anisochromines and most congrogadines) or six (*Assiculus*) infraorbital bones. (The noteworthy exception is the congrogadine genus *Rusichthys*, where only infraorbital bone 1 is present, and it does not communicate with the remainder of the cephalic lateral-line system.) Within the Pseudoplesiopinae, the reduction (through loss of the canal) and loss of infraorbital 2 are here regarded as an ordered transformation series. The reduction or loss of the second infraorbital in *Pectinochromis* and *Chlidichthys* is associated with the absence of a suborbital laterosensory pore that is present at the posterior opening of the second infraorbital in the remaining pseudoplesiopine genera. Instead, one or a series of superficial neuromasts are present between the tips of the first and third infraorbitals (Fig. 12D,E).

Character 27. Laterosensory-canal-bearing bones weakly developed. The laterosensory-canal-bearing bones of *Lubbockichthys, Pseudoplesiops* and *Amsichthys* are relatively well ossified, usually with well-developed laminar edges (Figs. 9A–C, 10A–C; state 0), as they are in the outgroup taxa (at least in adult specimens). In contrast, those of *Chlidichthys* and *Pectinochromis* are relatively weakly ossified, often with slit-like openings extending along the bones, and without well-developed laminar edges (Figs. 9D,E, 10D,E; state 1). We consider the latter apomorphic within the Pseudoplesiopinae.

Character 28. Second preopercular pore absent. Lubbockichthys has 6–11, rarely 6 (six only in small specimens) and *Pseudoplesiops* has 6–8, rarely 6 or 8, preopercular pores, with the upper two pores relatively closely spaced (Fig. 12A,B; state 0). *Pectinochromis* and *Chlidichthys* usually have only six preopercular pores (occasional specimens of both genera may have seven pores on one or both sides, but the configuration of upper pores is the same as in specimens with six pores), with the upper pore well separated from the lower pores (Fig. 12D,E; state 1). The relatively low number of pores is here argued to have resulted from the loss of the homologue of the second pore of the seven-pored genera, which results in the upper two pores being well separated from each other. *Amsichthys* also usually has only six pores (Fig. 12C), but the arrangement is here argued to be non-homologous with that

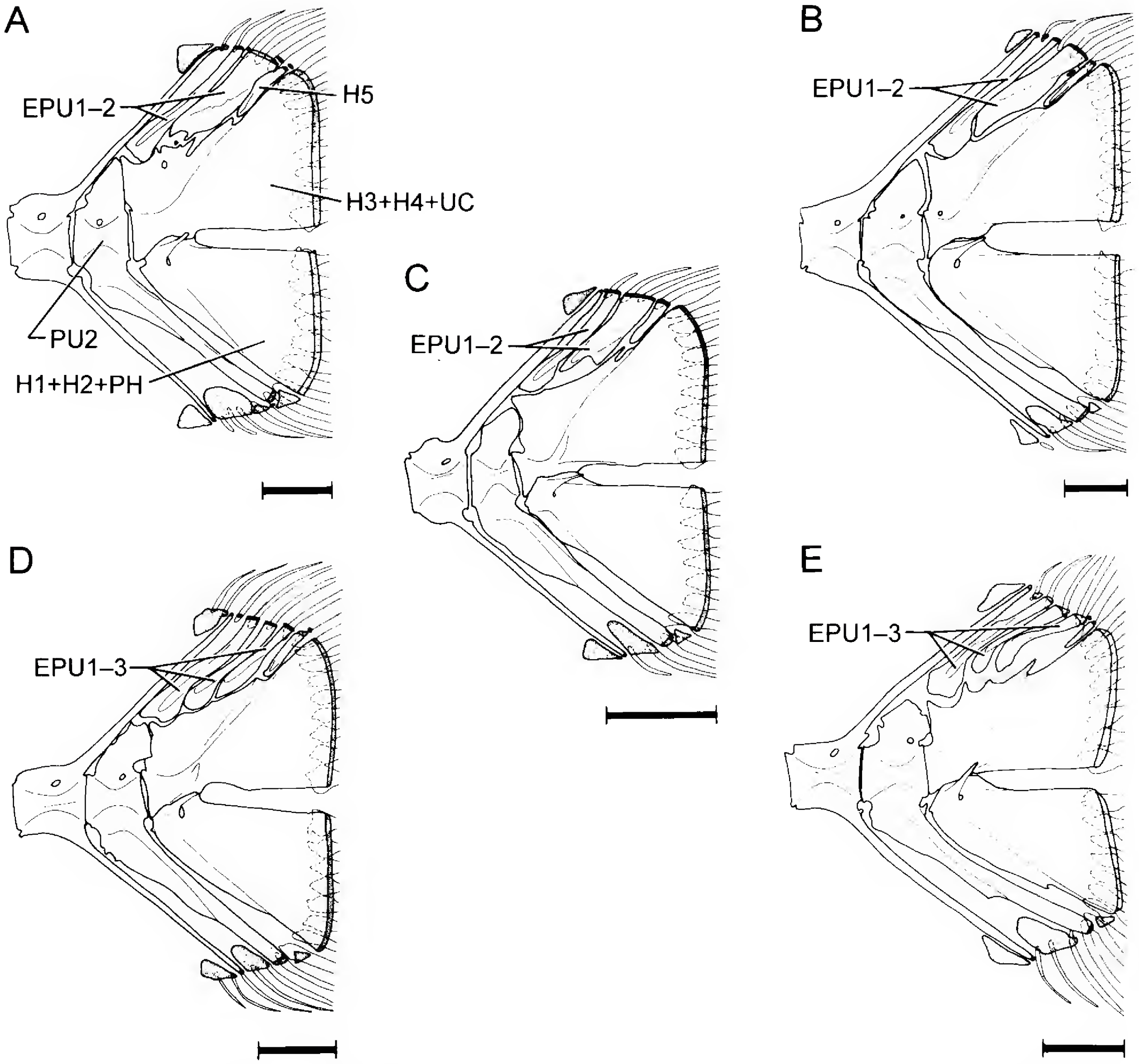


Figure 14. Caudal skeletons of selected pseudoplesiopine species in left lateral view: A, *Lubbockichthys* sp. 1, AMS I.25107-067, 47.3 mm SL; B, *Pseudoplesiops typus*, AMS I.19442-013, 50.6 mm SL; C, *Amsichthys knighti*, AMS I.22612-034, 28.3 mm SL; D, *Chlidichthys johnvoelckeri*, CAS 35451, 37.9 mm SL; E, *Pectinochromis lubbocki*, BPBM 28119, 35.5 mm SL (paratype). Cartilage shown in dense stipple; overlapping portions of fin-ray bases shown in broken lines. Abbreviations: EPU1-3, epurals 1–3; H1+H2+PH, fused hypurals 1 and 2 and parhypural; H3+H4+UC, fused hypurals 3 and 4 and compound urostylar complex; H5, hypural 5; PU2, preural centrum 2. Scale bars = 1 mm.

of *Chlidichthys* and *Pectinochromis* (see Character 12 above). The outgroup taxa have the upper two preopercular pores relatively close together, and most have relatively high numbers of preopercular pores: 12–16 for anisochromines; 10–19 for *Assiculoides*; and 9–18 for *Assiculus*. Congrogadines usually have only six or seven preopercular pores (nine in the relatively derived species *Halidesmus polypterus*), but the upper two pores are not widely separated. Therefore, the condition shown in *Chlidichthys* and *Pectinochromis* is considered apomorphic within the Pseudoplesiopinae.

Character 29. Ten precaudal vertebrae. Lubbockichthys, Amsichthys and almost all *Pseudoplesiops* species have more than ten precaudal vertebrae (Table 2; state 0), as do most of the immediate outgroup taxa: 12–19 in congrogadines; 11–12 in *Assiculoides*; and 11 in *Assiculus*. *Chlidichthys* and *Pectinochromis* are unusual among pseudoplesiopines in having ten precaudal vertebrae (Table 2; state 1). Anisochromines, one relatively derived *Pseudoplesiops* species and most pseudochromines (the only exceptions are *Assiculoides, Assiculus* and *Labracinus*) also have ten precaudal vertebrae. However, parsimony dictates that the presence of ten precaudal vertebrae is apomorphic within the Pseudoplesiopinae.

Character 30. Eye large. Most pseudoplesiopines have relatively small eyes: 8.5–10.6% SL in *Chlidichthys*, 7.9–11.7% SL in *Lubbockichthys*, and 8.2–11.0% SL in *Pseudoplesiops* (state 0). *Pectinochromis* and *Amsichthys* are distinctive in having relatively large eyes, 10.5–11.9 and 9.9–12.5% SL, respectively (state 1); overlap with smaller-eyed taxa can largely be attributed to ontogenetic variation (smaller specimens have proportionally larger eyes). Outgroup taxa have relatively small to moderate eyes; the condition shown by *Amsichthys* and *Pectinochromis* is therefore considered apomorphic.

Character 31. Dorsal-fin-ray branching. Pseudoplesiops, Amsichthys and *Chlidichthys* have mostly simple (unbranched) segmented dorsal-fin rays (state 0). *Lubbockichthys* and *Pectinochromis* have mostly branched segmented dorsal-fin rays (state 1). The first outgroup has mostly branched rays in this fin, whereas the second and third outgroups have mostly simple rays in the dorsal fin. Polarisation of this character is therefore equivocal within the Pseudoplesiopinae.

Character 32. Segmented anal-fin rays mostly simple. Lubbockichthys and *Pectinochromis* have mostly branched segmented anal-fin rays, as do the outgroup taxa (state 0). Conversely, the remaining pseudoplesiopine genera have mostly simple segmented anal-fin rays (state 1). The latter condition is therefore apomorphic within the subfamily.

Results of Parsimony Analysis. Phylogenetic analysis of the 32 characters (Table 1) resulted in the single tree shown in Fig. 15: tree length = 36; consistency index = 0.91; retention index = 0.76. [A second analysis was also performed using only characters 20–32, with character 26 recoded as "1" for *Chlidichthys*. In so doing, untested characters (synapomorphies of the Pseudoplesiopinae, and unique, unequivocal generic autapomorphies) were excluded. The analysis yielded the same tree, with the following statistics: tree length = 16; consistency index = 0.81; retention index = 0.76.].

Characters supporting monophyly of the Pseudoplesiopinae and its genera are discussed above in the diagnoses for the respective taxa.

Three synapomorphies support monophyly of a clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops*: segmented pelvic-fin rays all unbranched (character 20); posterior otic pores absent (character 21); and anterior temporal pores absent (character 22). One additional character, posterior interorbital pores (character 23), either supports monophyly of the clade (state 1), or is an autapomorphy of *Lubbockichthys* (state 0); the equivocal nature results from the presence of both states in the outgroup taxa (state 0 in the first outgroup, state 1 in the second and third outgroups), and the basal position of *Lubbockichthys* within the Pseudoplesiopinae. Similarly, mostly unbranched anal-fin rays (character 32) and mostly unbranched dorsal-fin rays (character 31), provide equivocal support for the clade consisting of *Chlidichthys, Amsichthys, Pectinochromis* and *Pseudoplesiops* (see below).

A single synapomorphy supports a sister-group relationship between *Amsichthys* and *Pseudoplesiops*: third supraneural bone well developed (character 24). However, as this character varies within *Pseudoplesiops*, and is intraspecifically variable in *C. abruptus*, support for this relationship is weak. The distribution of one other character, segmented anal-fin rays mostly simple (character 32), is equivocal; it either supports monophyly of *Amsichthys* + *Pseudoplesiops* (and occurs homoplastically in *Chlidichthys*), or diagnoses the more general clade that also includes *Chlidichthys* and *Pectinochromis*, with autapomorphic reversal in the latter genus. Mostly unbranched dorsal-fin rays (character 31) provides similar equivocal support for a sister relationship between *Amsichthys* and *Pseudoplesiops* (see below).

Five synapomorphies support a sister-group relationship between the Indian Ocean taxa *Chlidichthys* and *Pectinochromis*: three epurals (character 25); infraorbital 2 reduced or absent (character 26); laterosensory-canal-bearing bones weakly developed (character 27); second preopercular pores absent (character 28); and ten precaudal vertebrae (character 29).

Character 30—eyes large—is most parsimoniously interpreted as independently derived autapomorphies of *Pectinochromis* and *Amsichthys*.

The presence of mostly unbranched segmented dorsal-fin rays (character 31) has been cited as an autapomorphy of the Pseudoplesiopinae (Smith, 1954; Springer *et al.*,

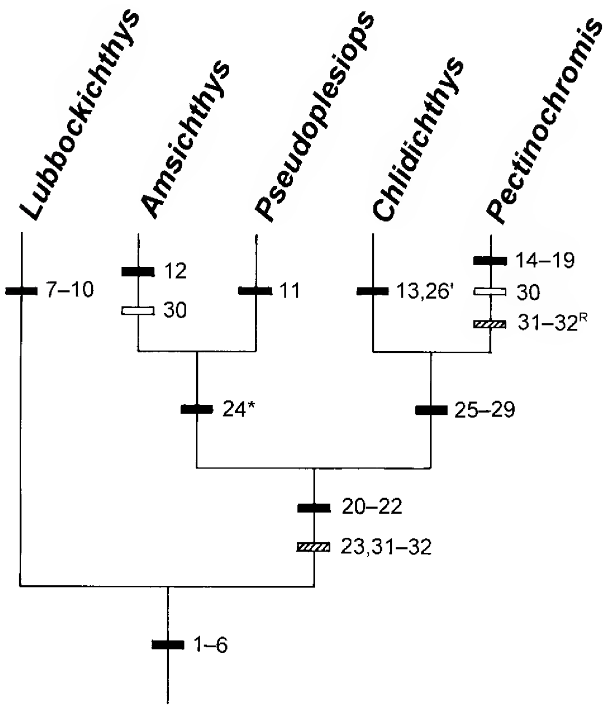


Figure 15. Cladogram of relationships between pseudoplesiopine genera generated from matrix in Table 1. Numbers indicate characters that support relationships (see text for details): solid bars indicate uncontradicted synapomorphies; open bars indicate homoplastic characters with unequivocal optimisations; hatched bars indicate homoplastic characters with equivocal distributions (see text for alternative optimisations); R indicates characters that reverse; * indicates characters that reverse within some derived (non-basal) species in terminal taxa; ' indicates derived state of multistate character.

Table 2. Comparison of selected characters of pseudoplesiopine genera. * Anterior extent of predorsal scalation is expressed in terms of proximity of anterior edge of first scale to either interorbital or supratemporal laterosensory commissure.

genus	dorsal-fin rays	anal-fin rays	pectoral-fin rays	pelvic-fin rays	total caudal-fin rays	vertebrae	anterior extent of predorsal scalation*	scales in lateral series
Amsichthys	I,23–24	I–II,13–15	16–18	I,4	24–25	11 + 18	interorbital	30–33
Chlidichthys	II,21–24	II–III,12–15	16–19	I,4	25–29	10 + 17–19	supratemporal to interorbital	37–52
Lubbockichthys	II,24–26	II,14–16	16–19	I,4	24–27	12–14 + 17–19 = 30–32	supratemporal	51–66
Pectinochromis	II,22–23	II,12–13	16–17	I,4	22–24	10 + 16–17	interorbital	35–39
Pseudoplesiops	I–II,22–29	I–III,13–18	15–18	I,3–4	23–26	10–14 + 17–21 = 28–33	supratemporal to interorbital	26–42

1977; Godkin & Winterbottom, 1985). However, the present analysis reveals that this character is homoplastic, with both character states occurring within the subfamily and its immediate outgroups. There are three equally parsimonious optimisations of the character, none of which provides support for monophyly of the Pseudoplesiopinae: (1) rays mostly branched (state 1) a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with reversal to mostly unbranched rays (state 0) in the clade consisting of *Amsichthys, Chlidichthys, Pectinochromis* and *Pseudoplesiops*, and autapomorphic acquisition of mostly branched rays in *Pectinochromis* (accelerated transformation optimisation); (2) independent acquisition of branched rays in Anisochrominae + Congrogadinae, *Lubbockichthys* and *Pectinochromis* (delayed transformation optimisation); and (3) mostly branched rays a synapomorphy of the Anisochrominae + Congrogadinae + Pseudoplesiopinae clade, with independent reversal to mostly unbranched rays in *Chlidichthys* and in the clade consisting of *Pseudoplesiops* and *Amsichthys*.

ACKNOWLEDGMENTS. We thank the following for the loan of specimens for this paper: J.T. Williams, S. Jewett (USNM), H.K. Larson (NTM), M. McGrouther, S.E. Reader, T. Trnksi (AMS), P.C. Heemstra (RUSI), J.E. Randall, A. Suzumoto (BPBM), D. Catania, W.N. Eschmeyer (CAS); W. Saul (ANSP), R. Winterbottom, M. Rouse (ROM); G.R. Allen, J.B. Hutchins, S. Morrison (WAM). S. Davidson and A.-M. Hine assisted with radiography and clearing and staining of specimens. P. Crabb photographed the specimens in Figs. 1–5. M.P.J. van Oijen provided a translation of Bleeker's description of *Pseudoplesiops typus*. G.D. Johnson, R.D. Mooi, J. Radding, D.J. Siebert, V.G. Springer, and R. Winterbottom discussed various aspects of this study. Manuscript drafts were read by, and improved by helpful comments from J.M. Leis, R.D. Mooi, N.R. Merrett and two anonymous reviewers.

References

Allen, G.R., 1987. Descriptions of three new pseudochromid fishes of the genus *Pseudoplesiops* from Australia and surrounding regions. *Records of the Western Australian Museum* 13(2): 249–261.

Berg, L.S., 1940. Classification of fishes both Recent and fossil. *Travaux de l'Institut Zoologique de l'Akadémie des Sciences de l'URSS* 5(2): 87–517.

Bleeker, P., 1858. Bijdrage tot de kennis der vischfauna van den Goram Archipel. *Naturrkundig Tijdschrift Nederlandsch Indië* 15: 197–218.

Bleeker, P., 1875. Sur la famille des Pseudochromoïdes et révision de ses espéces insulindiniennes. *Verhandelingen der Koninklijke Akademie van Wetenschappen, Amsterdam* 15: 1–32, pls 1–3.

Boulenger, G.A., 1895. *Catalogue of the Perciform Fishes in the British Museum. Second Edition. Volume 1*. London: Trustees of the British Museum.

Boulenger, G.A., 1899. Matériaux pour la fauna du Congo. Cinquième Partie. Cyprins, Silures, Cyprinodontes, Acanthoptérygiens. *Annales du Musée du Congo, ser. zool.* 1: 97–128, pls 40–47.

Boulenger, G.A., 1901. Notes on the classification of teleostean fishes.—I. On the Trachinidae and their allies. *Annals and Magazine of Natural History* (7) 8: 261–271.

Boulenger, G.A., 1902. Contributions to the ichthyology of the Congo.—II. On a collection of fishes from the Lindi River. *Proceedings of the Zoological Society of London* 1902(1): 265–271, pls 28–30.

Böhlke, J.E., 1960. Comments on serranoid fishes with disjunct lateral lines, with the description of a new one from the Bahamas. *Notulae Naturae of the Academy of Natural Sciences of Philadelphia* 330: 1–11.

Dingerkus, G., & L.D. Uhler, 1977. Enzyme clearing of alcian blue stained whole vertebrates for demonstration of cartilage. *Stain Technology* 52: 229–232.

Edwards, A.J., & J.E. Randall, 1983. A new dottyback of the genus *Pseudoplesiops* (Teleostei: Perciformes: Pseudochromidae) from the Red Sea. *Revue Française d'Aquariologie Herpétologie* 9(4): 111–114.

Farris, J.S., 1988. "Hennig86, Version 1.5," Program and documentation. New York: Farris, Port Jefferson.

Fowler, H.W., 1931. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the families Pseudochromidae, Lobotidae, Pempheridae, Priacanthidae, Lutjanidae, Pomadasyidae, and Theraponidae, collected by the United States Bureau of Fisheries steamer "Albatross", chiefly in Philippine seas and adjacent waters. *United States National Museum Bulletin* 100(11): 1–388.

Fowler, H.W., 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas.

Proceedings of the Academy of Natural Sciences Philadelphia 85: 354–357.

Gill, A.C., 1998. Homology of the anterior vertebrae, ribs, and dorsal fin pterygiophores and rays in congrogadine fishes (Perciformes: Pseudochromidae). *Copeia* 1998(4): 1041–1045.

Gill, A.C., & G.R. Allen, 1996. *Pseudochromis viridis*, a new species of dottyback from Christmas Island, Indian Ocean (Teleostei: Perciformes: Pseudochromidae). *Revue Française d'Aquariologie Herpétologie* 23(1–2): 33–38.

Gill, A.C., & J.B. Hutchins, 1997. *Assiculoides desmonotus*, new genus and species of dottyback from the Kimberley coast of Western Australia (Teleostei: Perciformes: Pseudochromidae). *Revue Française d'Aquariologie Herpétologie* 24(1–2): 43–48.

Gill, A.C., & R.D. Mooi, 1993. Monophyly of the Grammatidae and of the Notograptidae, with evidence for their phylogenetic positions among perciforms. *Bulletin of Marine Science* 52(1): 327–350.

Gill, A.C., & J.E. Randall, 1994. *Chlidichthys cacatuoides*, a new species of pseudoplesiopine dottyback from southern Oman, with a diagnosis of the genus *Chlidichthys* Smith, and new record of *Pseudochromis punctatus* Kotthaus from Oman (Teleostei: Perciformes: Pseudochromidae). *Revue Française d'Aquariologie Herpétologie* 21(1–2): 11–18.

Gill, A.C., J.E. Randall & A.J. Edwards, 1991. *Pseudoplesiops collare*, a new species of fish from Indonesia, with lectotype designation for *Nematochromis annae* Weber (Perciformes: Pseudochromidae: Pseudoplesiopinae). *Revue Française d'Aquariologie Herpétologie* 18(3): 75–78.

Godkin, C.M., & R. Winterbottom, 1985. Phylogeny of the family Congrogadidae (Pisces; Perciformes) and its placement as a subfamily of the Pseudochromidae. *Bulletin of Marine Science* 36(3): 633–671.

Günther, A., 1860. *Catalogue of the Acanthopterygian Fishes in the Collection of the British Museum. Volume second. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae*. London: Trustees of the British Museum.

International Commission on Zoological Nomenclature, 1986. Opinion 1417. *Chromis* Cuvier *in* Desmarest, 1814 (Osteichthyes, Perciformes): gender confirmed as feminine. *Bulletin of Zoological Nomenclature* 43(3): 267–268.

Johnson, G.D., 1984. Percoidei: development and relationships. In *Ontogeny and Systematics of Fishes*, eds. H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall Jr. & S.L. Richardson, pp. 464–498. American Society of Ichthyologists and Herpetologists Special Publication No. 1. Lawrence: Allen Press.

Jordan, D.S., 1923. A classification of fishes including families and genera as far as known. *Stanford University Publications, University Series, Biological Sciences* 3(2): 77–243+i–x.

Leviton, A.E., R.H. Gibbs Jr., E. Heal & C.E. Dawson, 1985. Standards in herpetology and ichthyology: part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985(3): 802–832.

Lubbock, R., 1975. Fishes of the family Pseudochromidae (Perciformes) in the northwest Indian Ocean and Red Sea. *Journal of Zoology, London* 176: 115–157.

Lubbock, R., 1976. Fishes of the family Pseudochromidae (Perciformes) in the central Indian Ocean. *Journal of Natural History* 10: 167–177.

Lubbock, R., 1977. Fishes of the family Pseudochromidae (Perciformes) in the western Indian Ocean. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* 35: 1–21, pls 1–5.

McAllister, D.E., 1968. Evolution of branchiostegals and classification of teleostome fishes. *National Museum of Canada Bulletin* 221: 1–239.

Mooi, R.D., 1993. Phylogeny of the Plesiopidae (Pisces: Perciformes: Percoidei) with evidence for the inclusion of the Acanthoclinidae. *Bulletin of Marine Science* 52(1): 284–326.

Mooi, R.D., [1996]. Revision, phylogeny, and discussion of biology and biogeography of the fish genus *Plesiops* (Perciformes: Plesiopidae). *Royal Ontario Museum Life Science Contributions* 159: 1–108. [Publication dated 1995, but actually published January 1996.]

Norman, J.R., 1966. *A Draft Synopsis of the Orders, Families and Genera of Recent Fishes and Fish-like Vertebrates*. London: Trustees of the British Museum (Natural History).

Pellegrin, J., 1904. Contribution á l'étude anatomique, biologique et taxinomique des poissons de la famille des Cichlidés. *Mémoires de la Société Zoologique de France* 16(3–4): 41–400, pls 4–7.

Potthoff, T., 1984. Clearing and staining techniques. In *Ontogeny and Systematics of Fishes*, eds. H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall Jr. & S.L. Richardson, pp. 35–37. American Society of Ichthyologists and Herpetologists Special Publication No. 1. Lawrence: Allen Press.

Regan, C.T., 1913. The classification of the percoid fishes. *Annals and Magazine of Natural History* (8)12: 111–145.

Roberts, C.D., 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science* 52(1): 60–113.

Schultz, L.P., 1943. Fishes of the Phoenix and Samoan Islands collected in 1939 during the expedition of the U.S.S. "Bushnell." *United States National Museum Bulletin* 180: 1–316.

Schultz, L.P., 1953. Family Pseudochromidae, pp. 380–411, pl. 33a. In: Schultz, L.P., E.S. Herald, E.A. Lachner, A.D. Welander & L.P. Woods, Fishes of the Marshall and Marianas Islands. Volume 1. Families from Asymmetrontidae through Siganidae. *United States National Museum Bulletin* 202: 1–685.

Smith, J.L.B., 1953. *The Sea Fishes of Southern Africa. Third Edition*. Cape Town: Central News Agency Ltd.

Smith, J.L.B., 1954. Pseudoplesiopsine fishes from South and East Africa. *Annals and Magazine of Natural History* (12)7: 195–208.

Springer, V.G., C.L. Smith & T.H. Fraser, 1977. *Anisochromis straussi*, new species of protogynous hermaphroditic fish, and synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae. *Smithsonian Contributions to Zoology* 252: 1–15.

Stiassny, M.L.J., & J.A. Moore, 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph intrarelationships. *Zoological Journal of the Linnean Society* 104: 209–242.

Taylor, W.R., 1967. An enzyme method of clearing and staining small vertebrates. *Proceedings of the United States National Museum* 122: 1–17.

Weber, M., 1913. *Die Fische Der Siboga-expedition. Siboga Expeditie LVII*. Leiden: E.J. Brill.

Weber, M., & L.F. de Beaufort, 1929. *The Fishes of the Indo-Australian Archipelago. V*. Leiden: E.J. Brill.

Weber, M., & L.F. de Beaufort, 1931. *The Fishes of the Indo-Australian Archipelago. VI*. Leiden: E.J. Brill.

Winterbottom, R., [1986]. Revision and vicariance biogeography of the subfamily Congrogadinae (Pisces: Perciformes: Pseudochromidae). *Indo-Pacific Fishes* 9: 1–34, pl. 1. [Publication dated 1985, but actually published February, 1986.]

Winterbottom, R., 1996. A new species of the congrogadin genus *Rusichthys* from southern Oman (Perciformes; Pseudochromidae), with notes on its osteology. *Canadian Journal of Zoology* 74(3): 581–584.

Winterbottom, R., & J.E. Randall, 1994. Two new species of congrogadins (Teleostei; Pseudochromidae), with range extensions for four other species. *Canadian Journal of Zoology* 72(4): 750–756.

Manuscript received 13 July 1998, revised 11 February 1999 and accepted 4 March 1999.

Associate Editor: J.M. Leis

© Copyright Australian Museum, 1999

Records of the Australian Museum (1999) Vol. 51: 161–168. ISSN 0067-1975

A New Species of *Graphium* Scopoli (Lepidoptera: Papilionidae) from the Bismarck Archipelago, Papua New Guinea

C.J. MÜLLER [1] AND W.J. TENNENT [2]

[1] Address for correspondence: P.O. Box 228, Dural NSW 2158, Australia

[1] Centre for Ore Deposit Research,
University of Tasmania, GPO Box 252-79, Hobart TAS 7001, Australia
cmuller@postoffice.utas.edu.au

[2] Biogeography and Conservation Laboratory, Department of Entomology,
The Natural History Museum, Cromwell Road, London SW7 5BD, England

ABSTRACT. *Graphium kosii* n.sp., a butterfly from high elevations in southern New Ireland, is described and figured. A key is presented for this and five closely related species: *Graphium weiskei* (Ribbe), *G. stresemanni* (Rothschild), *G. batjanensis* Okano, *G. macleayanum* (Leach) and *G. gelon* (Boisduval), all of which are confined to the Australasian region.

MÜLLER, C.J., & W.J. TENNENT, 1999. A new species of *Graphium* Scopoli (Lepidoptera: Papilionidae) from the Bismarck Archipelago, Papua New Guinea. *Records of the Australian Museum* 51(2): 161–168.

This paper is the first of two treating new butterflies from little known montane forests of New Ireland. It describes a new species of *Graphium*. New Ireland is a long (c. 400 km) ancient island arc situated northeast of New Britain (2°–4°S 151°–153°E). The highest land reaches 2399 m in the southern "Lak" district and represents eroded, andesitic volcanoes, approximately 25 million years old (Pigram *et al*., 1990). The biomes here are vertically diverse with lowland rainforest, mid and upper montane moss forest and a high montane heath vegetation, shown in Fig. 1 (McCallum & Sekhran, 1997). The International Conservation and Development Organisation (ICAD) attempted to procure the land proximal to the Weiten Rift Valley as World Heritage during 1992–1996 but terminated the project due to "land ownership difficulties" (P. Lavender, Pacific Heritage Foundation, pers. comm., 1998).

The "*weiskei*" group of butterflies within the genus *Graphium* comprises six closely related species: *G. macleayanum, G. weiskei, G. batjanensis, G. stresemanni, G. gelon* and the new species described here, *G. kosii* n.sp. All the species are restricted to the Australasian region, generally in and adjacent to mountainous areas. Saigusa *et al*., (1977) showed more general phylogenetic relationships of this group with *G. empedovana* (Corbet), *G. codrus* (Cramer), *G. sarpedon* (Linnaeus), and *G. cloanthus* (Westwood).

Graphium macleayanum occurs as four subspecies in eastern mainland Australia, Tasmania, and Lord Howe Island (Common & Waterhouse, 1981) and in highland Papua New Guinea (Sands & Fenner, 1978). The various subspecies differ generally in the extent of the green in the basal area on the forewing above. Specimens from Mount Ginini (Australian Capital Territory) are distinct from most others from southeastern Australia in that they are small (forewing c. 29 mm) with broad wings, stunted tails and extensive greenish colouring. In this respect they more closely resemble specimens of *G. m. moggana* Couchman from Tasmania.

Graphium weiskei is a striking, well-known butterfly represented by the nominotypical subspecies and *G. w. goodenovii* (Rothschild), in upland mainland New Guinea and Goodenough Island, respectively (Parsons, 1998). Niculescu (1977) raised a monotypic genus, *Klinzigia*, for *G. weiskei* based primarily on its distinctive genitalia. However, he did not consider the other closely related species and, since then, this genus has been synonymised with *Graphium* (e.g., Hancock, 1983; Parsons, 1998). Haugum & Samson (1981) retained this as a subgenus for the whole "*weiskei*" group. Parsons (1998) recognised five main male colour forms from a study of many *G. weiskei* specimens from eastern Papua New Guinea.

Graphium batjanensis was described by Okano (1984) from an unknown locality in Batjan Island, Moluccas, but "it would be undoubtedly in the mountain area of 1,000 m high in Batjan Is." (Okano, 1984). This species is fairly common in the high mountains of southern Batjan (A. Lambartan, pers. comm.). Hancock (1985) treated this as a distinct species, although Parsons (1998) considered it conspecific with *G. weiskei*. The specific status of *G. batjanensis* is accepted in this work (see discussion). Parsons (1998) suggested that *G. weiskei* will eventually be discovered on Halmahera Island.

Graphium stresemanni was described by Rothschild (1915) from a series collected at Manusela, Central Seram (Ceram), above 1,000 m elevation, in 1912. Okano (1983) stated that the type locality was at "3250 ft". This species is distinct in bearing a full row of subterminal spots on the hindwing upperside, and by the shape of the male valva (see Fig. 3b).

Graphium gelon is superficially unrelated to the other species within the "*weiskei*" group, bearing a resemblance to other *Graphium* species—*G. sarpedon* and *G. monticolus* (Fruhstorfer). The genitalia of *G. gelon*, however, place it clearly within this group (Saigusa *et al*., 1977). Okano (1984) illustrated the female genitalia and male valva of *G. gelon* but did not include those of the other species within the group. *Graphium gelon* is restricted to New Caledonia and the nearby Loyalty Islands (Holloway & Peters, 1976).

The new species, *Graphium kosii*, is so far only recorded from the high mountains of southern New Ireland, although it probably occurs on the Lelet Plateau, central New Ireland, where there has been a fleeting glimpse of "*G. weiskei* or a closely related species" (Parsons, 1998).

Materials and methods. This study was based on material borrowed from the following institutions.

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
BMNH	British Museum (Natural History), London
CJMC	private collection of C.J. Müller, Sydney
DHC	private collection of D. Hall, Sydney
EPC	private collection of Edward Petrie, Sydney
KONE	Department of Primary Industries, Konedobu, Papua New Guinea
RGC	private collection of R. Gotts, Winmalee, Australia
RMC	private collection of Russell Mayo, Newcastle, Australia
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden, Holland
SGC	private collection of S. Ginn, Sydney

Morphological terms and their abbreviations applied here conform with those used by Common & Waterhouse (1981).

Key to taxa within the "*weiskei*" species group of *Graphium*

1 Hindwing with tail at vein CuA1 vestigial/absent .... *Graphium gelon* (Boisduval)

—— Hindwing with tail at vein CuA1 well developed 2

2 Forewing above with basal area beneath cell cream/light green 3

—— Forewing above with basal area beneath cell shade of blue, blue-green, turquoise, mauve, purple and/or pink 6

3 Forewing above with only anterior half of cell green .... *G. macleayanum wilsoni* Couchman

—— Forewing above with cell entirely green 4

4 Beneath suffused yellowish .... *G. macleayanum insulana* (Waterhouse)

—— Beneath not suffused yellowish 5

5 Forewing above with basal area green beyond cell towards dorsum .... *G. macleayanum moggana* Couchman

—— Forewing above with basal area not green beyond cell . *G. macleayanum macleayanum* (Leach)

6 Hindwing vein M2 longer than forewing vein CuA2 7

—— Hindwing vein M2 shorter than forewing vein CuA2 8

7 Thoracic hairs ventrally light grey-brown .... *G. batjanensis* Okano

—— Thoracic hairs ventrally pink .... *G. kosii* n.sp.

8 Hindwing above with subterminal spots well developed .... *G. stresemanni* (Rothschild)

—— Hindwing above with subterminal spots absent or vestigial 9

9 Hindwing subtornal spots either side of vein CuA1 with length similar to width .... *G. weiskei weiskei* (Ribbe)

—— Hindwing subtornal spots either side of vein CuA1 with length much greater than width .... *G. weiskei goodenovii* (Rothschild)

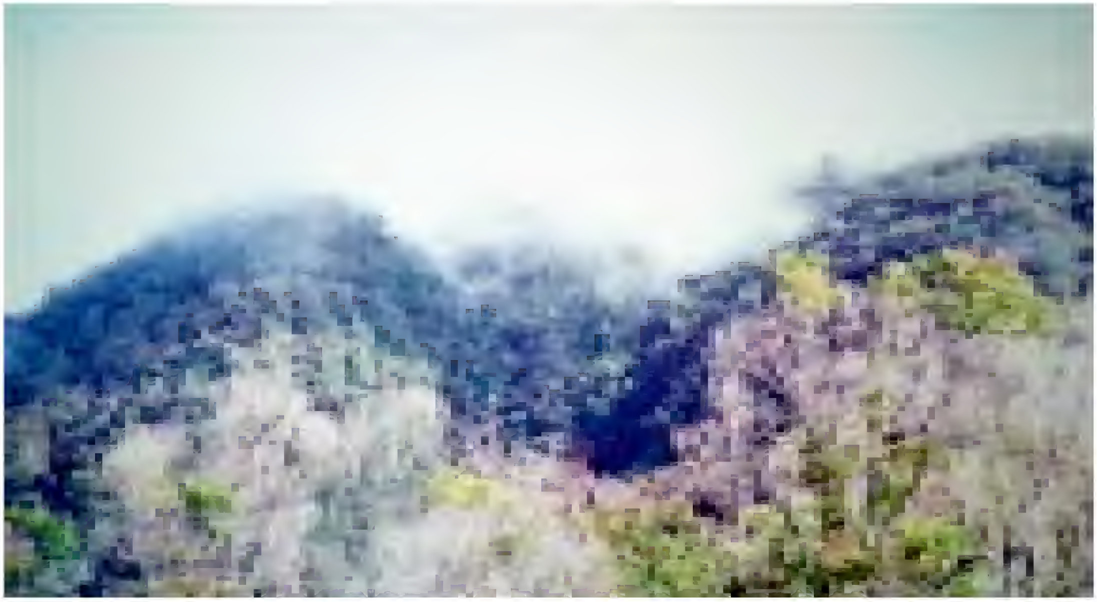


Figure 1. Hans Meyer Range southern New Ireland at 2300 m, c. 100 m below the summit—photograph of montane vegetation near the type locality.

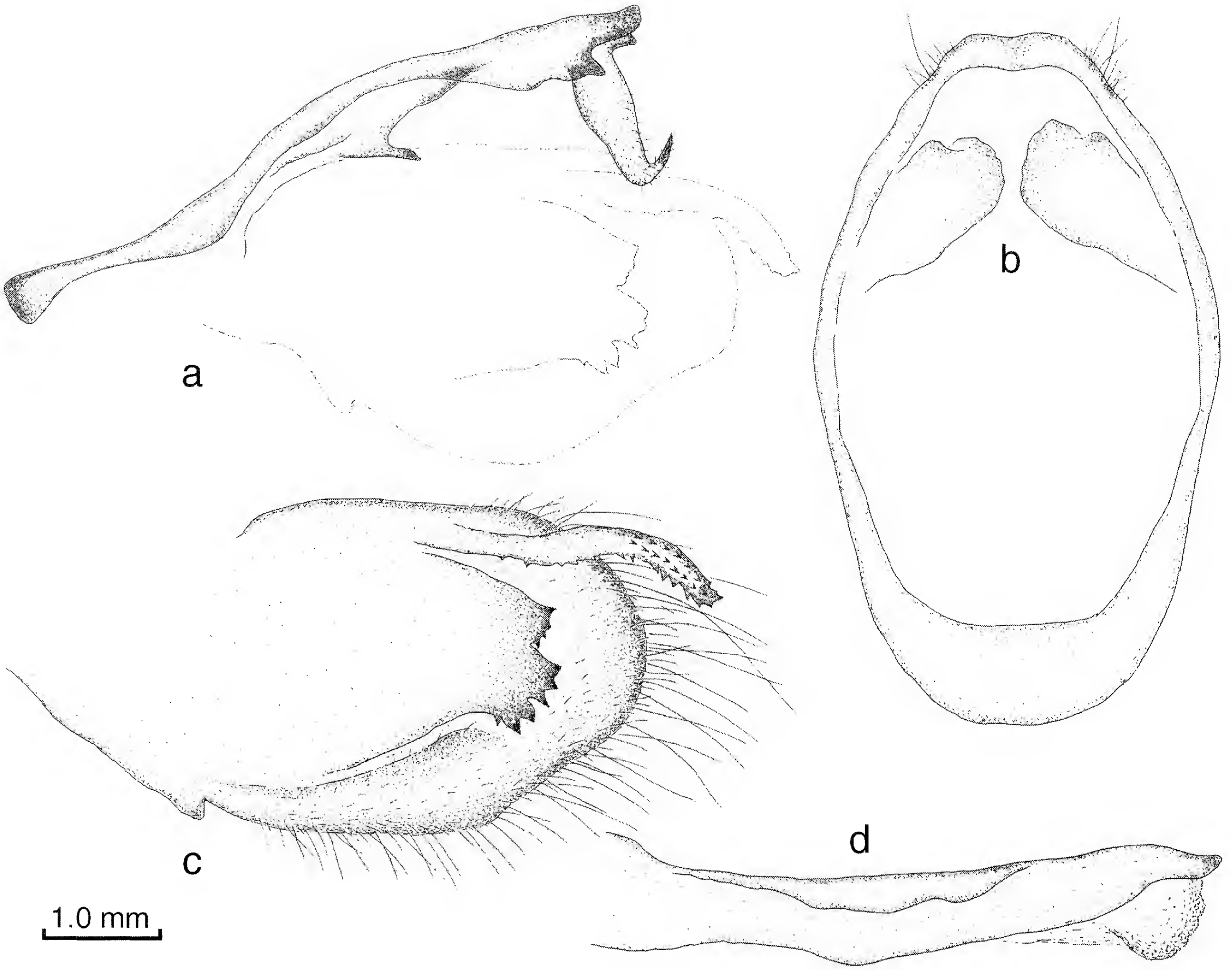


Figure 2. Male genitalia of *Graphium kosii* n.sp. (holotype ♂): a, lateral view; b, genitalic ring, dorsal view; c, left valva, lateral view; d, phallus, lateral view.

Graphium kosii n.sp.

Figs. 2a–d, 5–8

Type material. HOLOTYPE ♂, AM K111543, genitalia in vial attached to specimen in AM: "Lak district, Hans Meyer Range, 2400 m, S. New Ireland, 22 Aug. 1998, C.J. Müller". PARATYPES (44 ♂♂ and 5 ♀♀ all with same data as holotype unless otherwise indicated): 3 ♂♂ (one with genitalia dissected and attached to specimen) and 1 ♀ in ANIC; 3 ♂♂, 2 of which with genitalia dissected and attached to specimen and the third of which dated 20 August 1998, in BMNH; 3 ♂♂, 1 of which dated 20 August 1998 and 2 labelled "Lak district, Hans Meyer Ra., 1700 m, S. New Ireland, 18 Aug. 1998" in KONE; 3 ♂♂ (one with genitalia dissected and attached to specimen) in RNHL; 8 ♂♂ and 3 ♀♀, 4 of these 8 ♂♂ collected at an elevation at 1700 m and dated 18 August 1998 in CJMC; 15 ♂♂, 6 of which dated 20 August 1998, in DHC; 2 ♂♂ and 1 ♀ in SGC; 2 ♂♂ in RGC; 3 ♂♂, 1 of which dated 20 August 1998, in RMC; 2 ♂♂ in EPC.

Diagnosis. Forewing upperside basal and median markings brilliant turquoise, hindwings broad, ventral hairs on thorax and anterior segments of abdomen pink, genitalia with ring continuous, socii broad and simple, valva stepped.

Description. Male. (Figs. 5, 7). Head grey, covered with dense grey hairs above and pinkish-grey hairs beneath; antennae 19 mm long, brown, segmented deep brown-black, light brown ventrally, clubs broad and short, black dorsally and brown beneath; labial palpus, densely clothed with hairs, grey above, pinkish beneath. Thorax, densely haired, above grey-brown; beneath conspicuously greyish-pink; legs green. Abdomen, with thick hairs, deep grey-brown above and pinkish-brown beneath. Forewing 41.5 mm long, costa bowed strongly beyond postmedian area, termen straight between apex and vein M2, concave from vein M2 to CuA1, dorsum straight, above with ground colour black, a series of small, bluish-white submarginal spots from near costa to vein CuA2, congruent with termen except for proximal curve near apex; a large tear-shaped, dark green patch in postmedian area from, and normal to, costa to vein M2,

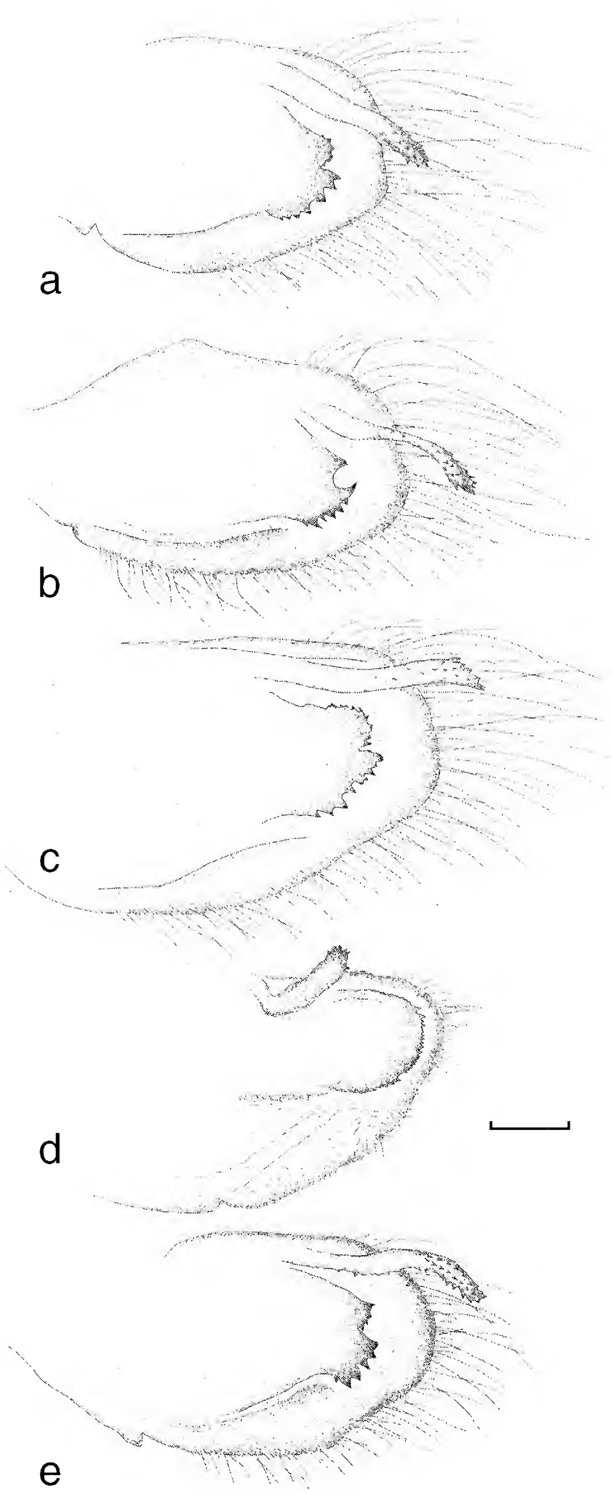


Figure 3. Lateral view of left valva. a, *G. weiskei* (Kerawagi, Papua New Guinea); b, *G. stresemanni* (Seram, Indonesia); c, *G. batjanensis* (Batjan, Indonesia); d, *G. macleayanum macleayanum* (Gosford, Australia); e, *G. kosii* n.sp. (New Ireland). Scale = 1.0 mm.

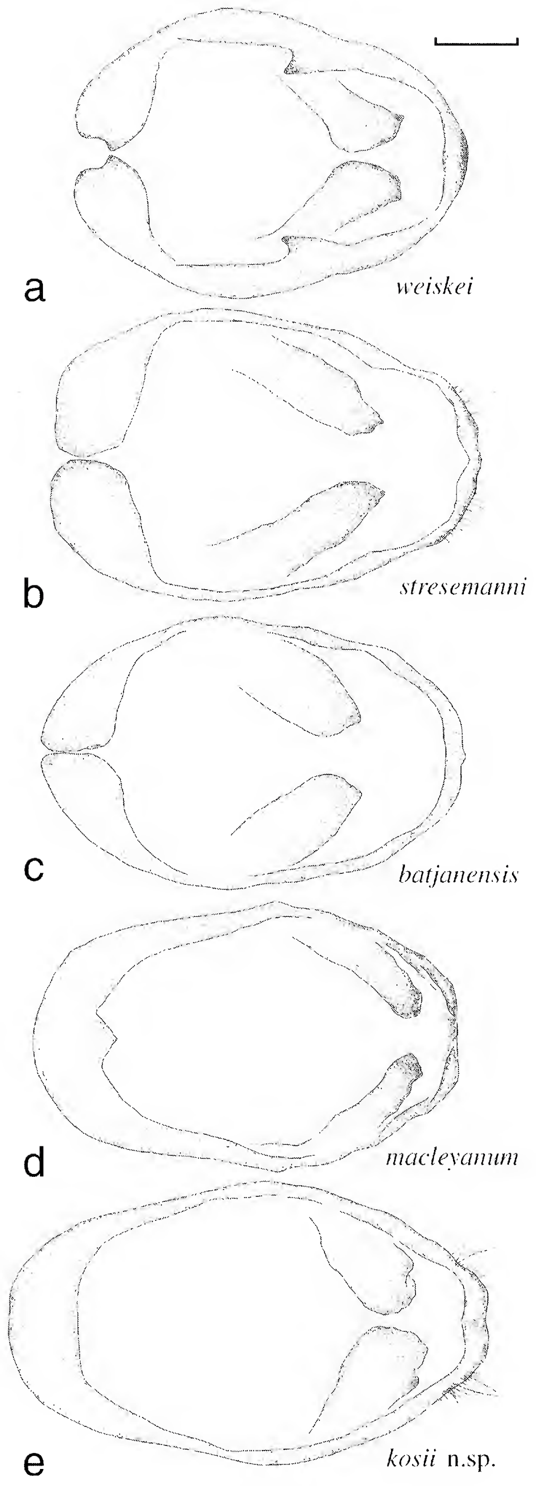
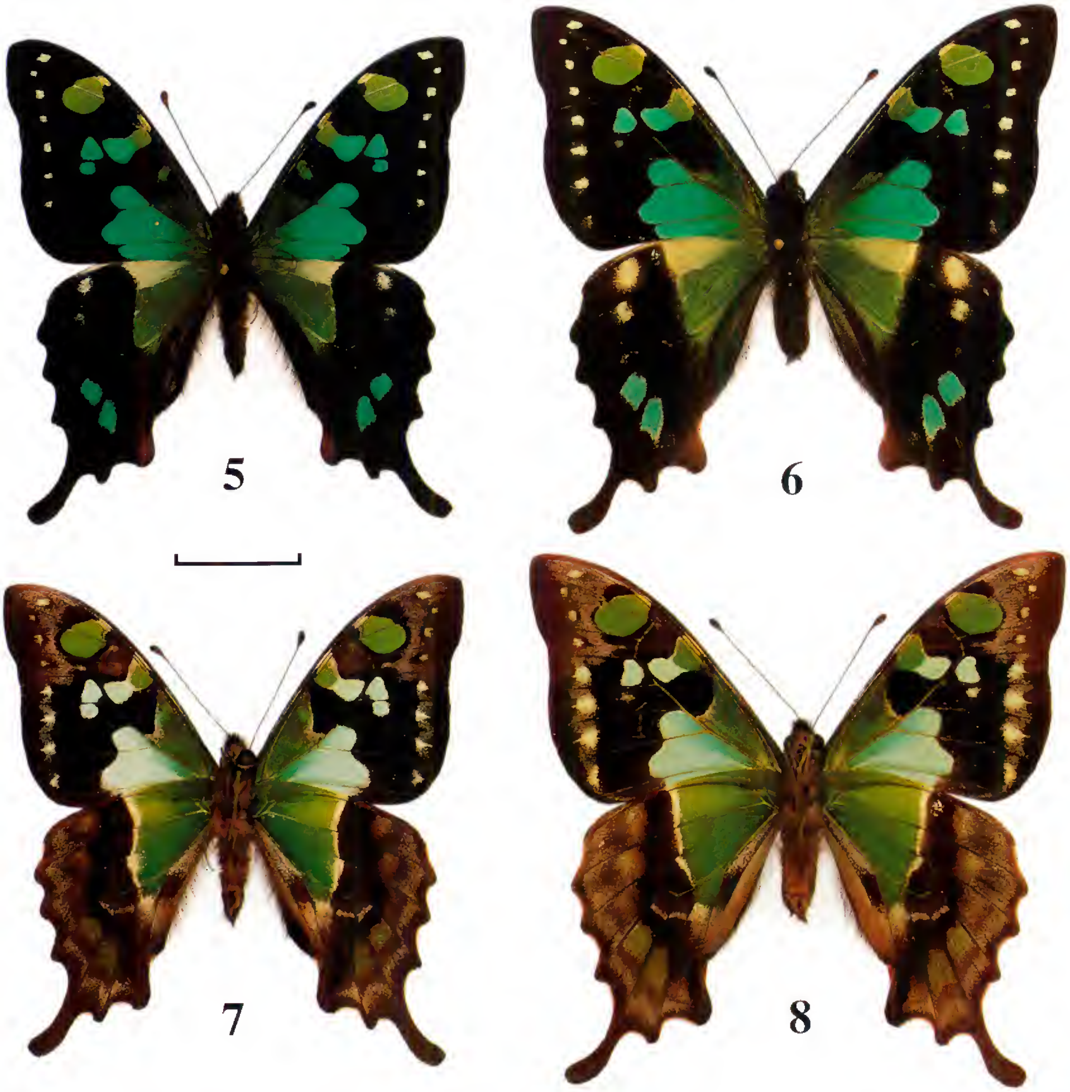


Figure 4. Dorsal view of male genitalic ring of *Graphium* species within the "*weiskei*" group, excluding *G. gelon*: a, *G. weiskei*; b, *G. stresemanni*; c, *G. batjanensis*; d, *G. macleayanum macleayanum*; e, *G. kosii* n.sp. Scale = 1.0 mm.



Figures 5–8. Adults of *Graphium kosii* n.sp. 3, holotype ♂ AM K111543, upperside; 4, paratype ♀ (CJMC), upperside; 5, holotype ♂, underside; 6, paratype ♀, underside. Scale = 20 mm.

intersecting veins white; a large "hour-glass" shaped marking in distal portion of cell approximately 1/5 distance from discocellulars to base, bright green in costal half and bright turquoise in remainder, two smaller turquoise spots in median area at end of cell to vein CuA1; a large basal turquoise area, below cell and vein CuA1, rounded distally between veins, basal portion of cell with obscure, deep green scales, often vestigial greenish-blue spot in middle of cell near costa, cilia narrowly black; beneath, ground colour brown in postmedian and apical area to vein M2, black in remainder, a series of small submarginal spots, greenish-white from apex to vein M2 and white and triangular in remainder, latter joined by scattered white scales; a postmedian patch near costa, shaped and coloured as above, median and basal pale markings shaped and positioned as in dorsal surface but bluish-white, costal half of "hour-glass" patch green; basal area with light blue scales below cell, large deep green area in cell, indented at lower half of cell in middle and tapered distally towards costa, white distal periphery, light brown scales in apical area tapering from costa to just beyond vein M3, cilia as above. Hindwing, narrow, with slightly spatulate tail at vein Cu A1, inner margin with fold supporting numerous dense grey sex hairs; lobed conspicuously at tornus, termen pronounced between veins; above ground colour black, deep green basal area from inner margin to junction of cell and veins Cu A2 and M2, concave at and white between vein Rs and costa, respectively; a small irregular white spot in apical area, vestigial blue spot beneath last spot; two turquoise tornal spots between veins M3 and Cu A2, well spaced, lower one larger and crescentic in shape, lobe chestnut brown, cilia pink or white; beneath, ground colour deep brown, darkening towards median area; a deep green basal area extending from bottom of cell and beyond, veins 1A+2A and Cu A2 and slightly bowed proximally to costa, narrowly crimson along costa at base and near apex; a white line of variable thickness separating basal area from brown distal 2/3 of hindwing; an acute, narrow white bar in median area

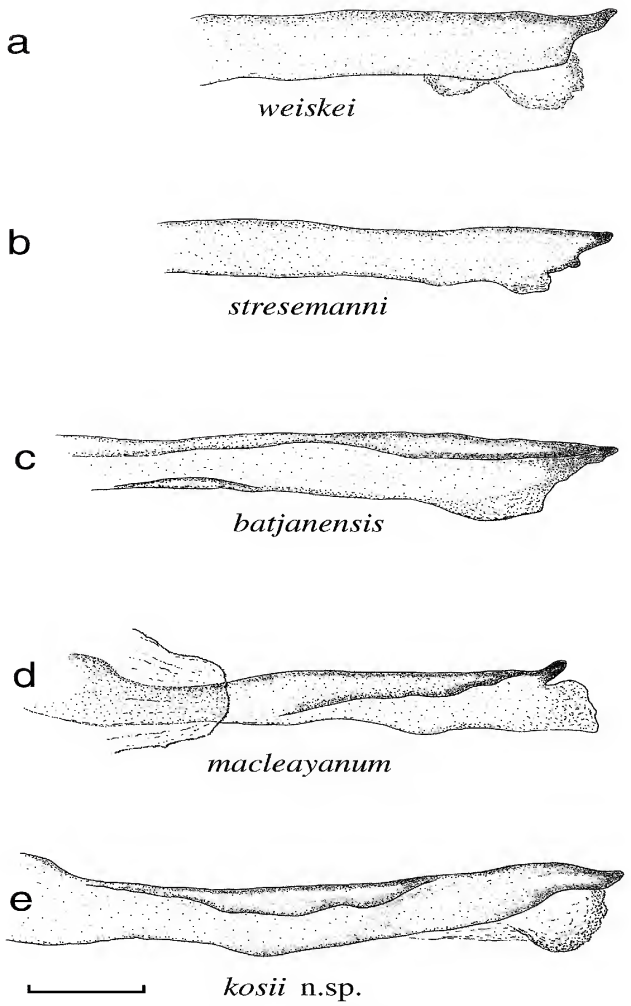


Figure 9. Lateral view of phallus of *Graphium* species within the "*weiskei*" group, excluding *G. gelon*: a, *G. weiskei*; b, *G. stresemanni*; c, *G. batjanensis*; d, *G. macleayanum macleayanum*; e, *G. kosii* n.sp. Scale = 1.0 mm.

between veins Cu A2 and M3, brownish-white scales between inner margin and cell, absent below junction of cell and vein 1A+2A, and also slightly bow-shaped brownish-white scales in submarginal area; vestigial bluish scales in tornal area identical in shape to tornal markings on upperside, cilia pink.

Female. (Figs. 6, 8). Similar to male but with both wings broader, submarginal spots in forewing much larger and whiter than in male, often extending to near dorsum; subapical white spots in hindwing upperside much larger and more obscure than in male, green and blue markings paler and slightly larger, postmedian spot below vein Cu A1 vestigial or absent; cell beneath with proximal green patch arcuate distally, submarginal markings beneath much paler than in male.

Male Genitalia. (Fig. 2). Genitalic ring long and continuous, oval-shaped, slightly concave anteriorly; socii broad; valva with ventrum straight, anteriorly toothed downward, aedeagus with anterior process.

Early stages. Unknown.

Measurements. Male forewing length 41.5 mm, antenna 19 mm; female forewing length 45 mm, antenna 21 mm.

Etymology. The new species name honours Tommy Kosi who, it is thought, collected the first specimens of this species.

Remarks. Only anecdotal information on Kosi's specimens can be found (L. Orsak, pers. comm., 1999). *Graphium kosii* n.sp. is the brightest species within the "*weiskei*" species group of *Graphium*. *Graphium kosii* may be readily separated from the other members of the species group by the colouration of the basal and median markings on the forewing above, which are deep turquoise, and by the broad hindwings which are only otherwise present in the Indonesian *G. batjanensis*. In addition, the hairs beneath the thorax and anterior segments of the abdomen are distinctly pink in *G. kosii*, a character developed elsewhere only in *G. macleayanum* and poorly in *G. weiskei*.

The genitalia of *G. kosii* provide useful diagnostic features in that the sociuncus ring is continuous and elongated posteriorly and the valva is distinctly stepped. Haugum & Samson (1981) recorded variability in the genitalia of *G. weiskei* but no such variability has been found among the five specimens of *G. kosii* examined, all of which fall outside the range of variation in the former species. The male genitalia of the other known species in the "*weiskei*" group are illustrated in Figs. 3–4.

ACKNOWLEDGMENTS. The authors are grateful to Max Moulds, Department of Entomology, Australian Museum, for making scientific equipment available for dissection and examination of genitalia. Dr Larry Orsak, Christensen Research Institute, Madang, kindly provided information on the origin of the first specimens of *G. kosii*. The expedition into remote southern New Ireland was possible thanks to the generous help of a number of local residents and the authors, particularly C.J.M., are grateful to all of them, especially Joel Todai, and others from Lak. The Department of Primary Industries, Namatanai, issued permits to acquire material.

References

Common, I.F.B., & D.F. Waterhouse, 1981. *Butterflies of Australia*. Revised edition. Sydney: Angus and Robertson.

Hancock, D.L., 1983. Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. *Smithersia* 2: 1–48.

Hancock, D.L., 1985. Notes on the taxonomy and distribution of the Indo-Australian Papilionidae (Lepidoptera). *Australian Entomological Magazine* 12: 29–34.

Haugum, J., & C.J. Samson, 1981. Notes on *Graphium weiskei*. *Lepidoptera Group of 1968, Newsletter* (Supplement) 1–12.

Holloway, J.D., & J.V. Peters, 1976. The butterflies of New Caledonia and the Loyalty Islands. *Journal of Natural History* 10: 273–318.

McCallum, R., & N. Sekhran, 1997. *Race for the Rainforest. Evaluating Lessons from an Integrated Conservation and Development "Experiment" in New Ireland, Papua New Guinea*. Papua New Guinea Biodiversity Conservation and Resource Management Programme, pp. 82.

Niculescu, E.V., 1977. Un nouveau genre de Graphiini: *Klinzigia* n. gen. (Lepidoptera: Papilionidae). *Bulletin, Société Entomologique de Mulhouse* 1977 (Oct–Dec): 51–52.

Okano, K., 1983. On the data of the type specimen of *Graphium stresemanni. Tokurana (Acta Rhopalocera)* 5: 88.

Okano, K., 1984. On the butterflies of "*Graphium weiskei*" group (Papilionidae) with description of a new species. *Tokurana (Acta Rhopalocera)* 8(1): 1–20.

Parsons, M.J.P., [1998]. *The Butterflies of Papua New Guinea. Their Systematics and Biology*. London: Academic Press. (Publication dated 1999).

Pigram, C.J., P.J. Davies, D.A. Feary, P.A. Symonds & G.C.H. Chaproniere, 1990. *Controls on the Tertiary Carbonate Platform Evolution in the Papuan Basin: New Play Concepts*. In *Petroleum Exploration in Papua New Guinea*, Proceedings of the First P.N.G. Petroleum Convention, Port Moresby, 12–14 February 1990, eds. G.J Carman & Z. Carman, pp. 185–195. Port Moresby: P.N.G. Chamber of Mines and Petroleum.

Rothschild, W., 1915. Lepidoptera collected by the British Ornithologists' Union and Wollaston Expeditions in the Snow Mountains, southern Dutch New Guinea: Rep. Coll. Made by Brit. Ornith. Uni. Exp. & Wollaston Exp. Dutch N. Guinea, p. 4, pl. I, fig. 15.

Saigusa, T., A. Nakanishi, H. Shima & O. Yata, 1977. Phylogeny and biogeography of the subgenus *Graphium* Scopoli. *Cho Acta Rhopalocerologica* 1: 2–32. [Japanese]

Sands, D.P.A., & T.L. Fenner, 1978. New butterfly records from the New Guinea region. *Australian Entomological Magazine* 4: 101–108.

Manuscript received 8 January 1999, revised 20 June 1999 and accepted 13 July 1999.

Associate Editor: Daniel J. Bickel

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 169–177. ISSN 0067-1975

A New Species of *Cethosia* and a New Subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea

C.J. MÜLLER

Address for correspondence: P.O. Box 228, Dural NSW 2158, Australia
Centre for Ore Deposit Research, University of Tasmania, GPO Box 252-79, Hobart TAS 7001, Australia
cmuller@postoffice.utas.edu.au

ABSTRACT. Two butterflies *Cethosia vasalia* n.sp. (Nymphalidae) and *Delias messalina lizzae* n.subsp. (Pieridae) are described and figured from mid to high montane New Ireland. *Cethosia vasalia* n.sp. and *C. obscura* Guérin-Méneville are parapatric locally within the Bismarck Archipelago. These two species and their subspecies are compared in detail.

MÜLLER, C.J., 1999. A new species of *Cethosia* and a new subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea. *Records of the Australian Museum* 51(2): 169–177.

This paper is the second describing new butterflies from montane forests of New Ireland; geographic and locality information is given in the first (Müller & Tennent, 1999). The genus *Cethosia* Fabricius, which occurs from Sri Lanka and India, in the Andamans and Nicobars, through Southeast Asia to eastern Papua New Guinea and northern Queensland, is represented by about ten species. Parsons (1989b, 1998) provided keys to the New Guinean genera of Heliconiinae, one of which is *Cethosia*. A new species, *Cethosia vasalia* n.sp., is described here from New Ireland. It superficially resembles *C. obscura* Guérin-Méneville, which occurs generally throughout the Bismarck Archipelago and together, these species are the most melanic in the genus.

All stages of *Cethosia* species may be unpalatable to predators (see Parsons, 1998). Evidence of this is provided by the bright colouration of adults and larvae, the latter, where known, also being gregarious. Larvae of *Cethosia* are capable of moving very quickly and this may be a means of escaping from green tree ants (*Smaragdina* sp.) which frequent the fresh tips of their vine foodplants (Passifloraceae).

Butterflies belonging to the genus *Delias* Hübner are commonly known as "jezebels" and are popular with enthusiasts worldwide, owing to their generally bright ventral surfaces. To date there are 236 species described (G.J.M. Gerrits, pers. comm., 1998); the majority occur within mainland New Guinea where there appears to have been explosive speciation in the Tertiary, possibly due to a complex geological evolution of that island. Elsewhere, members of this genus are distributed from the Himalayas through Southeast Asia to New Guinea, Solomon Islands, Vanuatu, New Caledonia and Australia. Numerous taxa exist to the west of New Guinea, whilst in the Bismarck Archipelago eight species are recorded and in the Solomon Islands only four species (Arora, 1983).

Most larval foodplants recorded for *Delias* butterflies are mistletoes (Loranthaceae), although many remain undocumented. A revision by Talbot (1928–1937) remains the principal work on this genus. Talbot's primary division was based on androconial form and wing pattern similarities and an extensive key was presented.

Materials and methods. This study was based on material borrowed from the following institutions.

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
BPBM	Bernice P. Bishop Museum, Honolulu
BMNH	British Museum (Natural History), London
CJMC	private collection of C.J. Müller
GJMGC	private collection of Fred Gerrits, Buderim, Australia
RGC	private collection of Robert Gotts, Winmalee, Australia
SGC	private collection of S.G. Ginn, Sydney

Morphological terms and their abbreviations applied here conform with those used by Common & Waterhouse (1981).

Taxonomy

Cethosia vasalia n.sp.

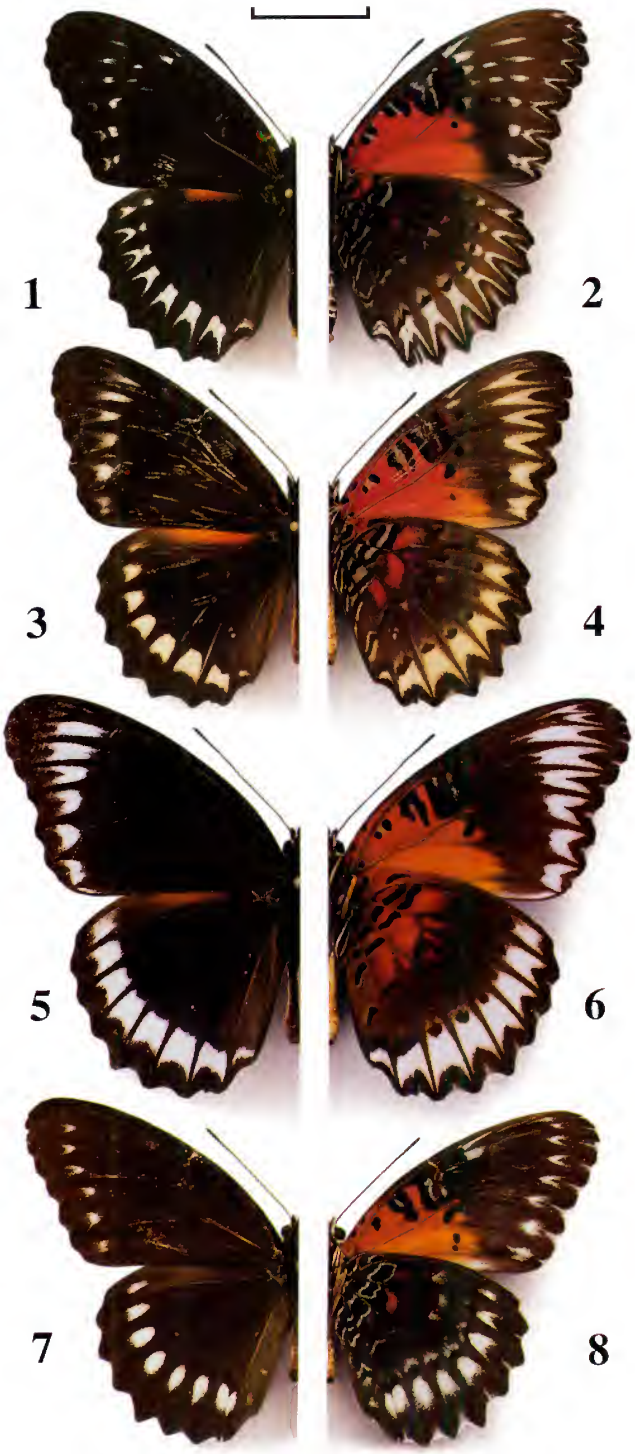
Figs. 1, 2, 9, 10, 17–19, 23, 27, 29

Type material. HOLOTYPE ♂, "Schleinitz Mts., Central New Ireland, 990 m, 26 July 1998, C.J. Müller" AM K111544, genitalia dissected and attached to specimen. PARATYPES (5 ♂♂, 4 ♀♀): 1 ♂ same data as holotype, genitalia slide No. 13097, ANIC; 1 ♂ same data as holotype, genitalia dissected and attached to specimen, BMNH; 2 ♀♀ labelled "New Ireland, Lelet Plateau, 1000 m, 2 Oct–18 Dec, 1963, W.W. Brandt, Sir E. Hallstrom", ANIC; 1 ♀ "New Ireland, December 1923 (A.F. Eichhorn)", BMNH; 1 ♂ same data as holotype, SGC; 2 ♂♂ same data as holotype except dated 23 July 1998, CJMC; 1 ♀ labelled "Hans Meyer Ra., S. New Ireland, 2300 m, 22 Aug. 1998, C.J. Müller", CJMC.

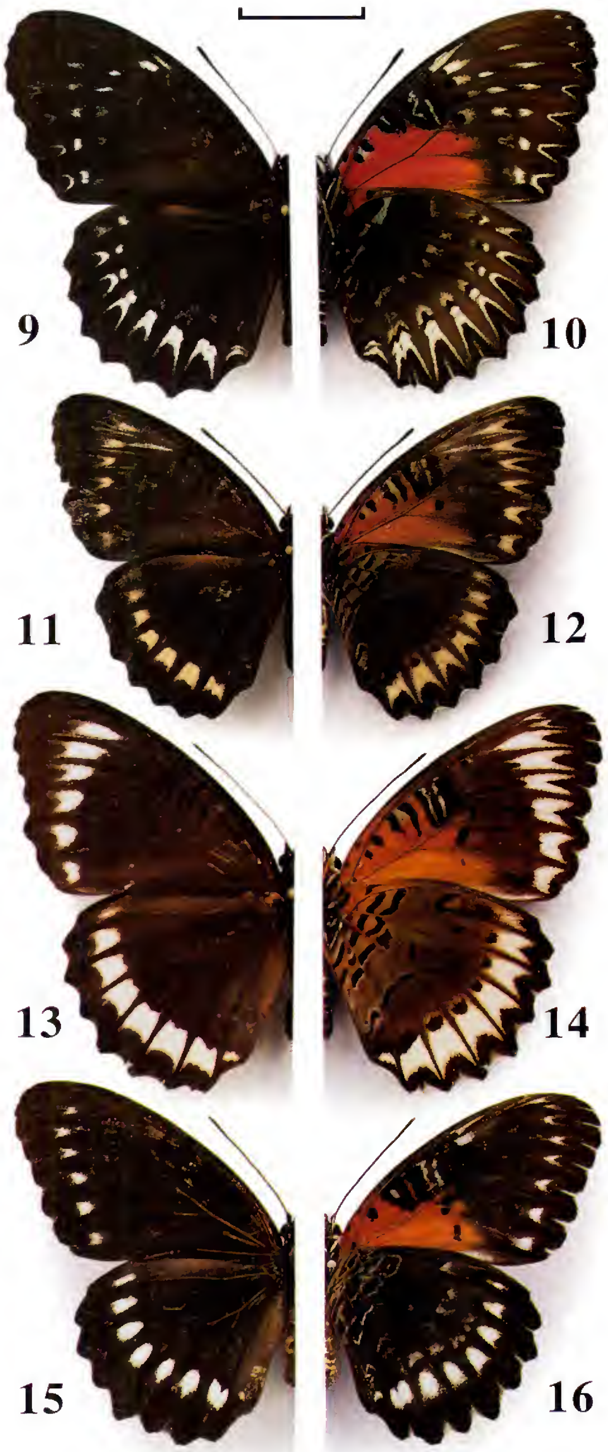
Diagnosis. Thorax and abdomen black. Mid-tibia with fine spines and narrow spurs, distally. Antennal clubs reaching well beyond discocellulars. Fore wings with four predominantly vestigial median to submarginal bands, pure white on upperside and extending conspicuously into hind wing as cusps, broken proximally toward the costa. Underside of hindwing, with mauve markings within the cell and between veins 1A+2A and Sc+R1, in median area. Genitalia with valvae closely spaced, sclerotised posterior hooks blunt and parallel, sociuncus anteriorly/laterally square-shaped with dorsoanterior process, strongly dipping, phallus blunt.

Description. Male. (Figs. 1, 2). Head black, with two pairs of white spots, adjacent to eye, dorsally and anteriorly; antennae long, black with deep brownish orange-tipped clubs, ventrally; labial palpus black with brown-black hair-tufts, beneath white, tending grey anteriorly. Thorax above black with fine brown-black hairs, beneath grey-black; legs deep grey, tending brown towards base, white posteriorly, mid-tibial spurs black, narrow. Abdomen black, beneath broadly segmented with white. Forewing with costa slightly bowed, termen conspicuously serrated between veins, slightly concave between veins M3 and tornus; above black with purple gloss from base to submarginal area; a series of white submarginal spots, cusp-shaped proximally, becoming vestigial towards apex; a band of irregularly shaped postmedian white spots, tending arcuate proximally towards costa; a pair of elongate white spots in postmedian and median area near costa; cilia broad, black at vein ends and white between; beneath with ground colour deep nut brown, basal area red, becoming orange near dorsum, forming an arcuate shape from inner margin about quarter of distance from tornus to distal part of cell to third distance along costa; a series of V-shaped white submarginal spots, becoming smaller towards apex; a further band of elongated, white postmedian spots, curving towards base near apex; two pairs of median spots between costa and vein Cu A1; vein M3 considerably bowed in median area beyond cell, inner row of white spots proximally bordered with elongate black spots, lowest reaching past vein Cu A1; two broad, irregular black bars either side of discocellulars, separated by grey-blue congruent but less extensive bars; two pairs of short, broad bars in upper one third of cell, each pair separated by grey-blue, short white bars between veins from termen to submarginal area; cilia as above. Hindwing, with termen indented between veins as in forewing, giving serrated appearance; above black with deep purple gloss from base to submarginal area; a series of crescent-shaped pure white submarginal spots, approximately congruent with termen, becoming smaller and divided towards costa; a restricted, subcostal purple-orange spot elongate between vein Rs and costa; inner margin grey; cilia as in dorsal surface of forewing; beneath, ground colour rich brown, deepening proximally; a series of white V-shaped submarginal markings, reaching to and slightly beyond row of irregular black markings in postmedian area, congruent with termen; a row of small black spots in median area, ringed narrowly with blue-grey, beyond bottom of cell only distally; a straight broad black bar near and normal to costa in median area; a series of three alternating pairs of black and blue-grey bars in basal area, basal of vein Sc+R1 black; a number of variable mauve spots in submedian area between veins 1A+2A and SC+R1; broad white bars reaching between veins from termen to submarginal area; cilia as above.

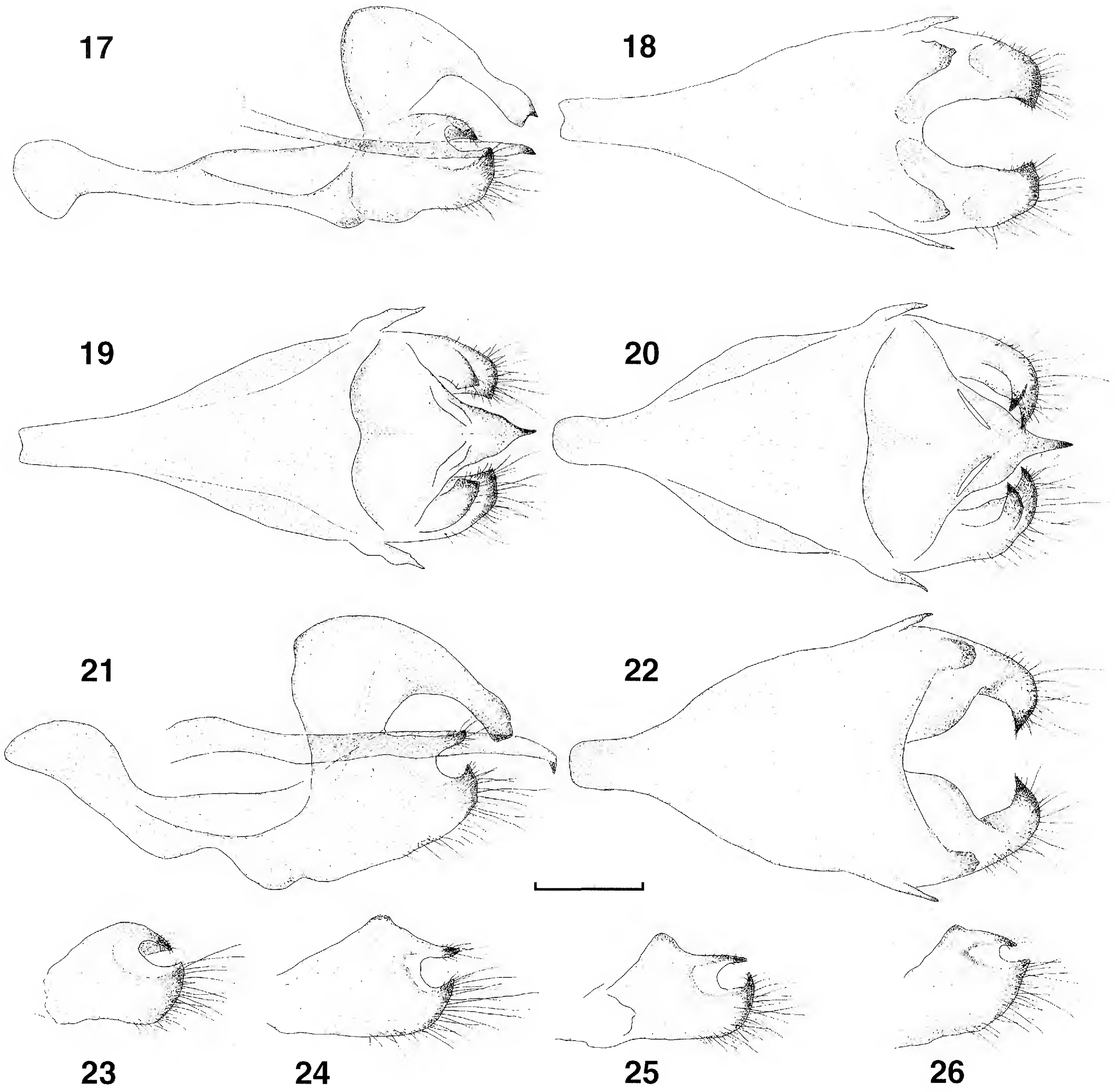
Female. (Figs. 9, 10). As in male but both wings broader with termen much more rounded; above with olive sheen replacing purple gloss in male; subcostal orange spot in hindwing very reduced and obscure; ground colour ventrally much greyer than in male; V-shaped markings with intracusp very dark and bisected by only narrow white lines, tapering basally; mauve median markings absent, replaced by broad black bars.



Figures 1–8. Adult males of *Cethosia* taxa from the Bismarck Archipelago. 1, *C. vasalia* n.sp., upperside (AM) (New Ireland); 2, *C. vasalia* n.sp., underside; 3, *C. obscura obscura* Guérin-Méneville, 1831, upperside (CJMC) (New Ireland); 4, *C. obscura obscura*, underside; 5, *C. obscura antippe* Grose-Smith & Kirby, 1889, upperside (CJMC) (New Britain); 6, *C. obscura antippe*, underside; 7, *C. obscura gabrielis* Rothschild, 1898, upperside (CJMC) (Manus Island); 8, *C. obscura gabrielis*, underside. Scale = 20 mm.



Figures 9–16. Adult females of *Cethosia* taxa from the Bismarck Archipelago. 9, *C. vasalia* n.sp., upperside (New Ireland); 10, *C. vasalia* n.sp., underside; 11, *C. obscura obscura*, upperside (New Ireland); 12, *C. obscura obscura*, underside; 13, *C. obscura antippe*, upperside (New Britain); 14, *C. obscura antippe*, underside; 15, *C. obscura gabrielis*, upperside (Manus Island); 16, *C. obscura gabrielis*, underside; all CJMC. Scale = 20 mm.



Figures 17–26. Male genitalia of *Cethosia* taxa from the Bismarck Archipelago. 17, *C. vasalia* n.sp., lateral view; 18, *C. vasalia* n.sp., ventral view; 19, *C. vasalia* n.sp., dorsal view; 20, *C. obscura obscura*, dorsal view; 21, *C. obscura obscura*, lateral view; 22, *C. obscura obscura*, ventral view; 23, *C. vasalia* n.sp., lateral view of right valva; 24, *C. obscura obscura*, lateral view of right valva; 25, *C. obscura antippe*, lateral view of right valva; 26, *C. obscura gabrielis*, lateral view of right valva. Scale = 1.0 mm.

Genitalia. (Figs. 17–19, 23). Uncus/tegumen rather narrow, uncus essentially square anteriorly but with sharp protrusion dorsally, dorsolateral flanges short and tapered, directed anteriorly, posteriorly concave in centre and bowed outwards dorsolaterally, laterally with deep, broad channels oval in shape; valva short and broad, sclerotised anteriorly with upper accessory dipping downward, dorsally parallel; vinculum saddle-shaped posteriorly; juxta short and blunt.

Early stages. Unknown.

Measurements. Male forewing length 44 mm, antenna 23 mm; female forewing length 48 mm, antenna 24 mm.

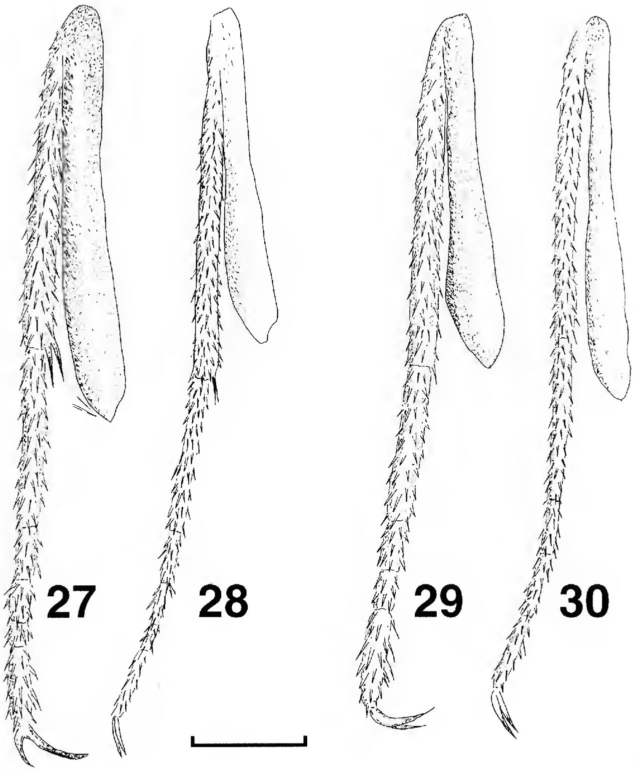
Remarks. *Cethosia vasalia* n.sp. is typical of the genus as shown by its characteristic terminal wing shape, serrated subterminal pattern on the underside of both wings and by the structure of the tarsal claws, which are long and simple (Figs. 27, 29) (see Parsons, 1998). The new species is superficially similar to *C. obscura* Guérin-Méneville (Figs.

3–8, 11–16, 20–22, 24–26, 28, 30), although displays several differences to that species. The antennae of *C. obscura* reach only barely beyond the distal part of the forewing cell whereas those of *C. vasalia* extend well past the discocellulars. The abdomen is orange-brown in *C. obscura* yet is always black in *C. vasalia*. Additionally, the legs in *C. vasalia* are much more robust and with well-developed tarsal spurs by comparison to *C. obscura* (Figs. 27–30). The patterns of both wings in *C. vasalia* are very distinctive, bearing four, mostly vestigial pure white, not dirty white to cream as in *C. obscura*, bands on both surfaces of the forewing and a costally bisected band on the hindwing, whilst in the various subspecies of *C. obscura*, only one well-developed band is present on both wings. Parsons (1998) figured a female from the W. Brandt collection held in ANIC (see Type material) as a "rare female form" of *C. obscura*. He separated this based on its pure white markings which are V-shaped and the overall dark appearance of the female. *Cethosia vasalia* is the darkest member of the genus. With no male material available until now, the species was considered a female form of the former species.

The male genitalia in the subspecies of *C. obscura* vary only slightly from one another in the shape of the valva (Figs. 24–26). In *C. vasalia*, the sociuncus apex is laterally square-shaped with a prominent upper spike, whilst in *C. obscura* it is saddle-shaped. The male valva in the latter species are widely spaced, unlike those in *C. vasalia* and possess long, tapering sclerotised hooks which are blunt and dorsally parallel in the new species. The vinculum is indented in *C. vasalia*, posteriorly, whilst in *C. obscura* it is rounded.

The parapatric distributions of *Cethosia vasalia* n.sp. and *C. obscura* Ribbe, on New Ireland is intriguing, considering the close affinities between the two taxa. Their occurrence in differing habitats with no obvious physical barriers has implications as to their possible evolution. Perhaps their separation may be postulated in a fashion similar to that for *Hypochrysops geminatus* Sands and its sister species, *H. pythias* (Lycaenidae) in mainland New Guinea. The former species does not occur below 1100 m although it is widely distributed on that island (Sands, 1986). *Hypochrysops pythias* is widespread in lowland regions from the Moluccas in eastern Indonesia to eastern mainland Papua and also in northern Queensland. Similarly, the highland species *C. vasalia* appears to exhibit a much more restricted distribution than the low altitude *C. obscura*, which occurs widely in the Bismarck Archipelago. Mainland New Guinea has experienced a structurally similar, although temporally distinct, geological evolution to that of New Ireland, the former being obducted above sea level fairly early in the Tertiary, c. 45 million years ago, whilst New Ireland became subaerial in the Miocene period, approximately 25 million years ago (Davies, 1990). Perhaps early influxes of each ancestral pair of species, here mentioned, became temporally isolated and fixed to the continual orogenesis, raising land in both islands. Subsequent waves possibly inhabited lower elevations and were adapted to different host plants at that stage. Sands (1986) records the larvae of *H. geminatus* on a *Commersonia* sp., different to the lowland and ubiquitous *C. bartramia* (L.) Merr., upon which the larvae of *H. pythias* feed (Common & Waterhouse, 1981; Sands, 1986). Parsons (1998) records *Adenia heterophylla* (Passifloraceae) as a host for *C. obscura* and the author observed females of *C. obscura* ovipositing on that plant at several locations in lowland New Ireland. Conversely, no plants of *A. heterophylla* were observed in the areas where *C. vasalia* was collected. It is possible that the larvae of *C. vasalia* feed on a species endemic to upland areas in New Ireland.

In central and southern New Ireland, *C. obscura* is not known to occur above approximately 500 m, while *C. vasalia* has been collected between 990 m and 2300m. South of Malum Village, central New Ireland, adults of both species were collected within 2 km of each other. *Cethosia o. obscura* is fairly common in lowland rainforest where it flies directly and quite rapidly, males within their territories often circle close to a vantage perch where they settle 2–6 m above the ground. Adults of *C. vasalia* were noted to fly rather more slowly than those of *C. obscura* and to settle frequently on the ground or on low vegetation. A further female specimen of *C. vasalia* was collected by the author in the Schleinitz Mountains at 990 m but was released, owing to its very poor condition.



Figures 27–30. Mid- and hind-legs of *C. vasalia* n.sp. and *C. obscura obscura*. 27, *C. vasalia* n.sp., mid-leg; 28, *C. obscura obscura*, mid-leg; 29, *C. vasalia* n.sp., hind-leg; 30, *C. obscura obscura*, hind-leg. Scale = 2.0 mm.

Delias messalina vigasa Parsons

Delias messalina naokomoritae Morita, 1995: 5, fig. 3, **n.syn.**

Delias messalina Arora, is a recently described species from the Solomon Islands. Arora (1983) described two subspecies, designating those from Bougainville (Papua New Guinea) as nominotypical; the other subspecies from Santa Isabel and Guadalcanal was named *orientalis*. Parsons (1989a) described *D. messalina vigasa* from eastern New Britain. *Delias m. naokomoritae* Morita, 1995 is clearly synonymous with *D. m. vigasa*. Both Parsons (1989a) and Morita (1995) described *D. m. vigasa* and *D. m. naokomoritae*, respectively, from two specimens. The holotype male of *vigasa* (BPBM) was used again for the description of *naokomoritae* and the names are therefore objective synonyms. Few specimens of *D. messalina* are known, in particular there are very few from the Bismarck Archipelago.

Arora (1983) suggested that *D. messalina* is closely related to *D. nigrina* (Fabricius) from eastern mainland Australia, although Parsons (1998) considered *D. messalina* to be more closely related to *D. weiskei* Ribbe from mainland New Guinea. Certainly, *D. nigrina* and *D. messalina* exhibit structural and behavioural similarities.

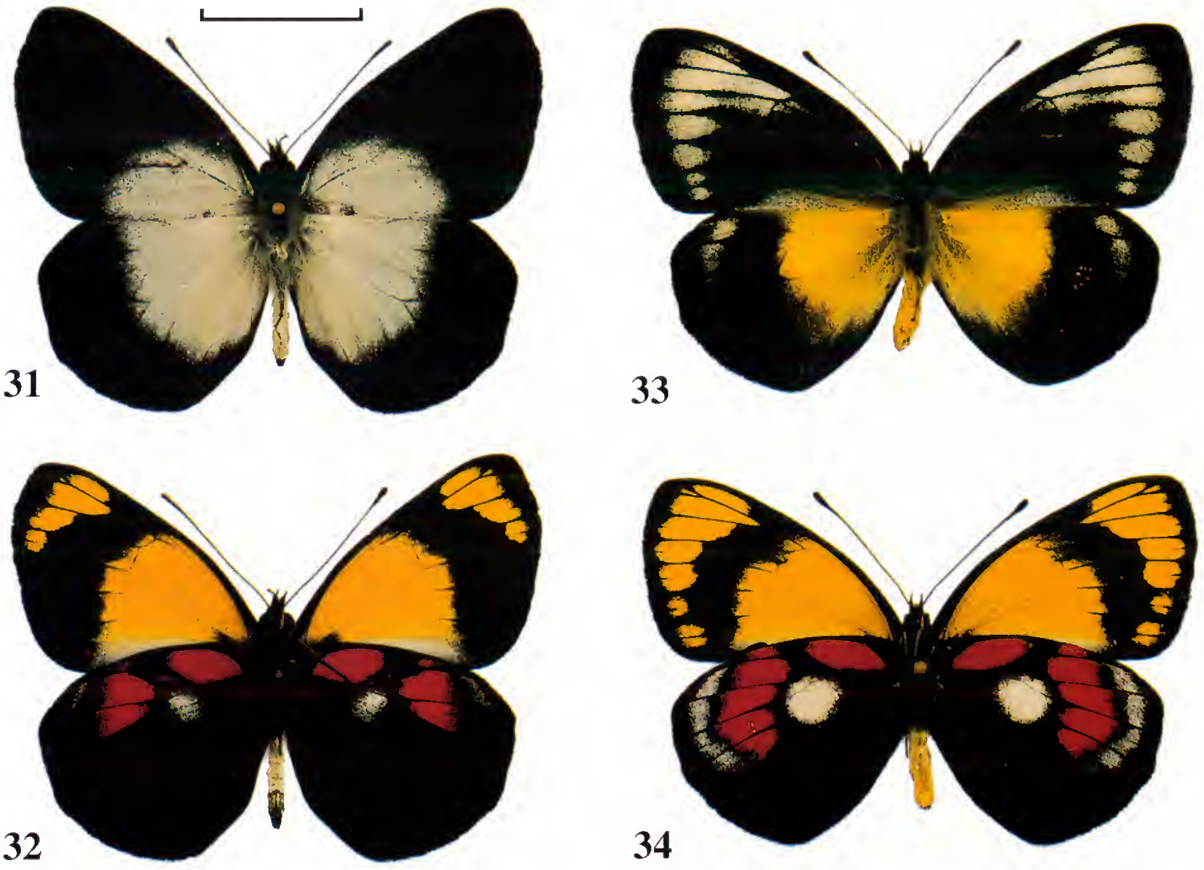
***Delias messalina lizzae* n.subsp.**

Figs. 31–38

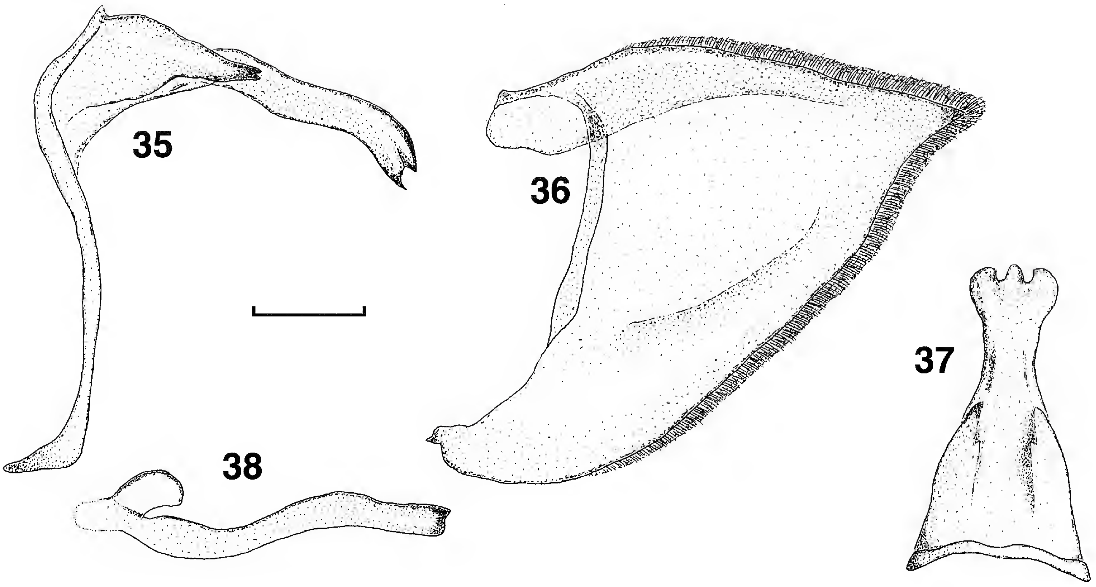
Type material. Holotype ♂, “Lak district, Hans Meyer Ra., S. New Ireland, 2400 m, 22 Aug. 1998, C.J. Müller” AM K111545, genitalia dissected and attached to specimen. Paratypes: 5 ♀♀, all with same data as holotype, 1 in RGC, 2 in GJMGC and 2 in CJMC.

Diagnosis. Thorax beneath black. Abdomen white in male, yellow in female. Male fore and hind wings somewhat pronounced at veins M2 and apex, respectively, ground colour above with greenish sheen. Female with forewing submarginal band extending to dorsum on both surfaces and often reaching cell on upperside. Vestigial pale spots also present at apex of hindwing. Underside of hindwing in both sexes with scarlet markings very broad, circular spot in cell pure white. Genitalia with median lobe of uncus, dorsally spaced from lateral lobes which are flattened anteriorly, valva narrow, with ventrum nearly straight.

Description. Male. (Figs. 31, 32). Head black, clothed with dense deep grey hairs; labial palpus black, eye ringed with pale yellow anteriorly; antenna black, tipped white ventrally.



Figures 31–34. Adults of *Delias messalina lizzae* n.subsp. 31, holotype ♂, upperside; 32, holotype ♂, underside; 33, paratype ♀ (CJMC), upperside; 34, paratype ♀ (CJMC), underside. Scale = 20 mm.



Figures 35–38. Male genitalia of *Delias messalina lizzae* n.subsp. 35, lateral view of genitalic ring; 36, lateral view of left valva; 37, dorsal view of uncus; 38, lateral view of phallus. Scale = 0.5 mm.

Figure 39. Hans Meyer Range, 2,000 m, southern New Ireland.

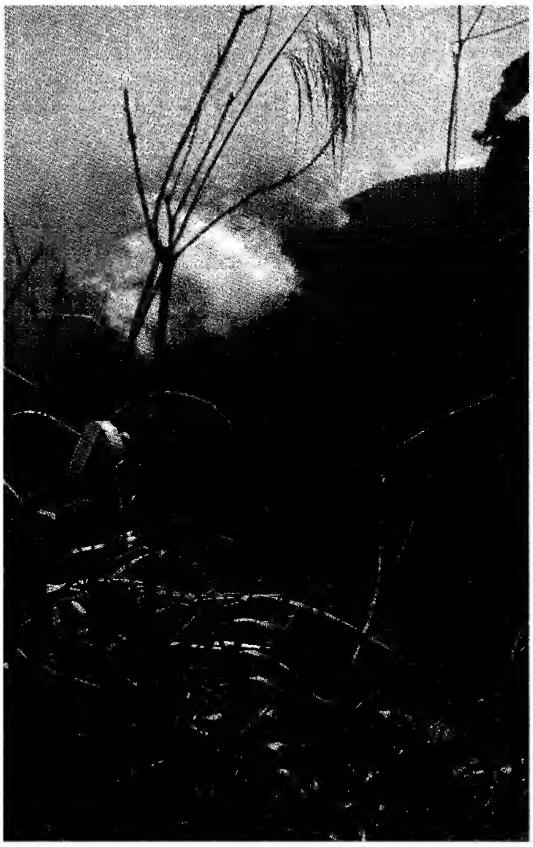


Figure 40. Hans Meyer Range, 1700 m, southern New Ireland.

Thorax black with long grey hairs dorsally, beneath black, legs black. Abdomen white, narrow black dorsal ridge, tapered posteriorly, claspers grey. Forewing with termen somewhat convex at vein M2; above with ground colour black with greenish sheen; basally light grey in an arcuate manner from approximately 1/8 along costa to junction of veins CuA1 and cell and to dorsum 1/4 of distance from apex; beneath black with bright yellow subapical band from costa to vein M3, vestigial between veins R3 and R4+5 and intruding abruptly between veins R3 and M2; base to postmedian area brilliant yellow, abruptly changing to white below vein 1A+2A; costa broadly black to vein Sc, black patch at base between cell and vein 1A+2A. Hindwing above with ground colours in dorsal surface of forewing; a large basal to median/postmedian light grey area extending from costa near apex to end of cell and to dorsum, about 2/3 of distance towards tornus, congruent with termen; beneath with ground colour black, an irregular small pure white spot in cell, approximately 2/3 distally; a large basal scarlet patch extending to vein Rs, rounded distally; a scattering of scarlet scales between veins Rs and M1; one vestigial and two large scarlet markings in median area between costa and M2, becoming irregular distally; a vestigial band of light grey scales near apex between veins Rs and M1.

Female. (Figs. 33, 34). Head, antennae, legs and labial palpus as in male. Thorax grey with dense yellow-grey hairs; beneath black. Abdomen yellow, with narrow black dorsal line, tapering posteriorly, beneath cream. Forewing, with costa and termen slightly bowed; dorsum straight; black above with deep greenish basal area, progressively becoming light grey and extending to postmedian area at dorsum; a well-developed series of white submarginal spots, elongate, especially between veins R4+5 and M3 and reaching into cell between veins M1 and M2, vestigial between veins R3 and costa, rounded distally; beneath black with pure white, circular spot in cell and reaching beyond intersections of veins Rs and M1; a large scarlet basal spot above cell and reaching vein Rs, a broad, conspicuous band of scarlet spots between costa and M3, in postmedian area; a band of silvery-grey markings from Sc+R1 to M3, elongate, approximately congruent with termen but running obliquely towards dorsum.

Genitalia. (Figs. 35–38). Uncus dorsally with median lobe separated from lateral lobes which are straight anteriorly, laterally with lower lobe downward dipping and tapered to a sharp point; valva fairly narrow and tapered to apex, ventrum nearly straight; ring concave ventrolaterally; juxta irregular and tapered ventrally.

Early stages. Unknown.

Measurements. Male forewing length 32 mm, antenna 17 mm; female forewing length 33 mm, antenna 18 mm.

Remarks. *Delias messalina lizzae* is a most striking member of the large genus *Delias* Hübner. The male of *D. m. lizzae* may be separated from those of other subspecies particularly by its rather acute wing shape and greenish gloss on the upperside of both wings. In addition, the pale basal area in both wings above is far more restricted than in other subspecies and is greyish in colour. Beneath, the hindwing bears large, bright red markings that are confined between the costa and vein M1. The male most closely resembles that of *D. m. vigasa* Parsons, ventrally, The female above is superficially most similar to *D. m. orientalis* Arora, although the white submarginal markings in the forewing of the former are very extensive and there is a greenish basal area. The hindwing above is bright yellow in the basal to median area and the subterminal spots near the apex are well developed. Beneath, the submarginal spots on the forewing are large and extend to the dorsum. The hindwing beneath bears a large pure white spot in the cell and the scarlet basal and median spots are very large.

The male genitalia of the new taxon are closer to *D. nigrina* than to the other subspecies of *D. messalina*, although the wing pattern is closer to *D. messalina*. In particular, the median lobe of the uncus is well separated from the lateral lobes and the valvae are much narrower with an almost straight ventrum.

Both sexes of the new taxon were observed and/or collected between 1400 m and 2400 m elevation, in the Hans Meyer Range, southern New Ireland. The biome here is one of high montane moss forest (Figs. 39, 40) and heathland, the latter is apparently peculiar to the upper peaks and ridges. Specimens of *D. m. lizzae* were collected above the canopy as they sailed with prevalent wind and were observed to fly as high as 60 m above the ground. Two females were observed flying high in the canopy (c. 30 m) at 1400 m apparently in search of oviposition sites. The type series of *D. m. vigasa* were collected between 1100 m and 1300 m in far eastern New Britain, although a further specimen in BPBM is labelled "New Britain Gazelle Pen. Talliligap, 300 m, 17–18.XII.1962"; "J. Sedlaceck Collector BISHOP" (Parsons, 1989a). The type series of *D. m. messalina* were collected by W.M. Brandt at Guava, Bougainville, at c. 1300 m and in Guadalcanal specimens of *D. m. orientalis* were collected at the summit of Mount Popomanaseu at 2327 m (Tennent, 1997).

ACKNOWLEDGMENTS. The author thanks Max Moulds, Department of Entomology, Australian Museum, for the use of dissecting equipment in his care. Gabriel Kolmau, Schleinitz Mountains, New Ireland, aided with transport in remote areas and Noah Lurang, New Ireland Provincial Government, provided documentation to access the Lak district, the author is grateful to both.

References

Arora, R., 1983. New *Delias* butterflies from the Solomon Islands (Lepidoptera: Pieridae). *Systematic Entomology* 8: 15–24.

Common, I.F.B., & G.A. Waterhouse, 1981. *Butterflies of Australia*. Revised edition. Sydney: Angus and Robertson.

Davies, H.L., 1990. Structure and evolution of the border region of New Guinea. In *Petroleum Exploration in Papua New Guinea*, eds G.J. Carman & Z. Carman, pp. 245–270. Port Moresby: P.N.G. Chamber of Mines and Petroleum.

Grose-Smith, H., & W.F. Kirby, [1889]. *Rhopalocera Exotica, Being Illustrations of New, Rare and Unfigured Species of Butterflies* (1887–1902).

Guérin-Méneville, F.E., [1831]. Insectes. In *Voyage Autour du Monde Execute par Ordre du Roi*, L.I. Duperry, p. 277. (1830–1838).

Morita, S., 1995. Two new subspecies of the genus *Delias* (Lepidoptera: Pieridae) from New Britain Is. and Bachan Is. *Futao* 20: 4–5.

Müller, C.J., & W.J. Tennent, 1999. A new species of *Graphium* Scopoli (Lepidoptera: Papilionidae: Papilioninae: Leptocircini) from the Bismarck Archipelago, Papua New Guinea. *Records of the Australian Museum* 51(2): 161–168. [This volume].

Parsons, M.J., 1989a. A new *Delias* subspecies, a new *Sabera*, and a new *Parantica* from Papua New Guinea (Lepidoptera: Pieridae, Hesperiidae, Nymphalidae). *Bishop Museum Occasional Papers* 29: 193–198.

Parsons, M.J., 1989b. Taxonomic studies in New Guinea and Solomons Nymphalidae (Lepidoptera: Rhopalocera), and discovery of abdominal scent organs in the females of various nymphalinae genera. *Bishop Museum Occasional Papers* 29: 174–192.

Parsons, M.J., [1998]. *The Butterflies of Papua New Guinea. Their Systematics and Biology*. London: Academic Press. (Publication dated 1999).

Rothschild, W., 1898. Some new Lepidoptera from the East. *Novitates Zoologicae* 5: 216–219.

Sands, D.P.A., 1986. A revision of the genus *Hypochrysops* C. & R. Felder (Lepidoptera: Lycaenidae). Leiden, Copenhagen: E.J. Brill, Scandinavian Science Press.

Talbot, G., 1928–37. A monograph of the pierine genus *Delias*, 6 parts, pp. iii + 656, London.

Tennent, W.J., 1997. The search for *Tiradelphe schneideri* Ackery & Vane-Wright, 1984 (Lepidoptera: Danainae). *British Journal of Entomology and Natural History* 10: 203–209.

Manuscript received 8 January 1999, revised 20 June 1999 and accepted 13 July 1999.

Associate Editor: Daniel J. Bickel.

© Copyright Australian Museum, 1999

Records of the Australian Museum (1999) Vol. 51: 179–186. ISSN 0067-1975

An Unusual Micromorphic Brachiopod from the Middle Cambrian of North-Eastern New South Wales, Australia

GLENN A. BROCK

Centre for Ecostratigraphy and Palaeobiology, Department of Earth and Planetary Sciences,
Macquarie University NSW 2109, Australia
Glenn.Brock@mq.edu.au

ABSTRACT. *Anomalocalyx cawoodi* new genus and new species, from Middle Cambrian (Floran-Undillan) allochthonous limestone clasts of the Murrawong Creek Formation, north eastern New South Wales, is characterised by a deep, tapering, conical ventral valve with a pair of simple teeth, an arched pseudodeltidium, well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, and a presumed calcium carbonate shell composition, all suggesting an affinity with the Brachiopoda. *Anomalocalyx cawoodi* also possesses a number of unusual morphological features including an elongate, tapering interior tube extending along the inner posterior margin of the ventral valve, under the pseudodeltidium, that may be interpreted as a spondylium. Though possible cnidarian and molluscan affinities are fully explored, the weight of available evidence suggests the affinities of *A. cawoodi* are with the Brachiopoda.

BROCK, GLENN A., 1999. An unusual micromorphic brachiopod from the Middle Cambrian of north-eastern New South Wales, Australia. *Records of the Australian Museum* 51(3): 179–186.

Williams *et al.* (1996) erected five new classes of brachiopods united by a number of shared synapomorphies within the subphylum Rhynchonelliformea including, (*a*) the presence of a pair of calcareous shells held together by an articulatory device at the posterior hinge line between the two shells, (*b*) an acoelomic pedicle core, and (*c*) the presence of a diductor system to control the opening of the shells. Williams *et al.* (1996) placed another calcareous class, the Craniata, characterised by a lack of articulation and functional pedicle, in a separate "inarticulate" subphylum. All five rhynchonelliform classes are represented in the Cambrian radiation and display a wide range of unusual morphological adaptations, particularly with regard to valve articulation, musculature and pedicle opening (Popov, 1992; Popov *et al.*, 1996; Williams *et al.*, 1996). Typical morphological variations manifest in these early groups include the development of simple, presumably primitive, articulation mechanisms as exemplified by early obolellids (such as *Bicia* Walcott), kutorginids and nisusiids (Roberts & Jell, 1990; Popov, 1992; Popov *et al.*, 1996), and the evolution of unique features in a number of short-lived taxa. Examples of such features include the unusual spoon-shaped apical plate and supporting pedestal in the ventral valve of the naukatid genera *Bynguanoia* Roberts (in Roberts & Jell, 1990) and *Oina* Popov & Tikhonov, 1990, the arcuate plate along the hingeline in the ventral valve of the monospecific taxon *Bajarinovia* Aksarina & Pelman, 1978, and the posterior plate or colleplax in chileids (Popov *et al*., 1996).

In addition to taxa that can, more or less, be comfortably placed within the concept of the phylum Brachiopoda (or Phylum Brachiozoa, subphylum Brachiopoda *sensu* Cavalier-Smith, 1998), there are a number of aberrant Cambrian organisms that secreted bivalved calcareous shells that cannot be placed in the Brachiopoda with any confidence. As an example, the Early Cambrian taxa *Apistoconcha* and *Aroonia* from the Flinders Ranges, South Australia (Conway Morris & Bengtson, in Bengtson *et al*., 1990), and *Tianzhushanella* from China (Lui, 1979), are brachiopod-like in possessing a pair of calcareous shells with a posterior hinge axis of articulation, and a plane of bilateral symmetry bisecting the midline of both valves. However, the overall form of the valves, and the unique nature of the articulatory mechanism in these taxa, led Conway Morris & Bengtson (in Bengtson *et al*., 1990: 184) to conclude that they were not true brachiopods, but possibly represented a sister lophophorate lineage. Parkhaev (1998) recently placed *Apistoconcha* and *Tianzhushanella* in a new Class, the Siphonoconcha, and suggested an affinity with the Mollusca or Stenothecoida, rather than with the Brachiopoda.

The focus of this paper is to describe the unique features of another aberrant calciate brachiopod taxon, from the Middle Cambrian Murrawong Creek Formation, northeastern New South Wales, Australia, and to probe the functional morphology and possible zoological affinities of this problematic organism.

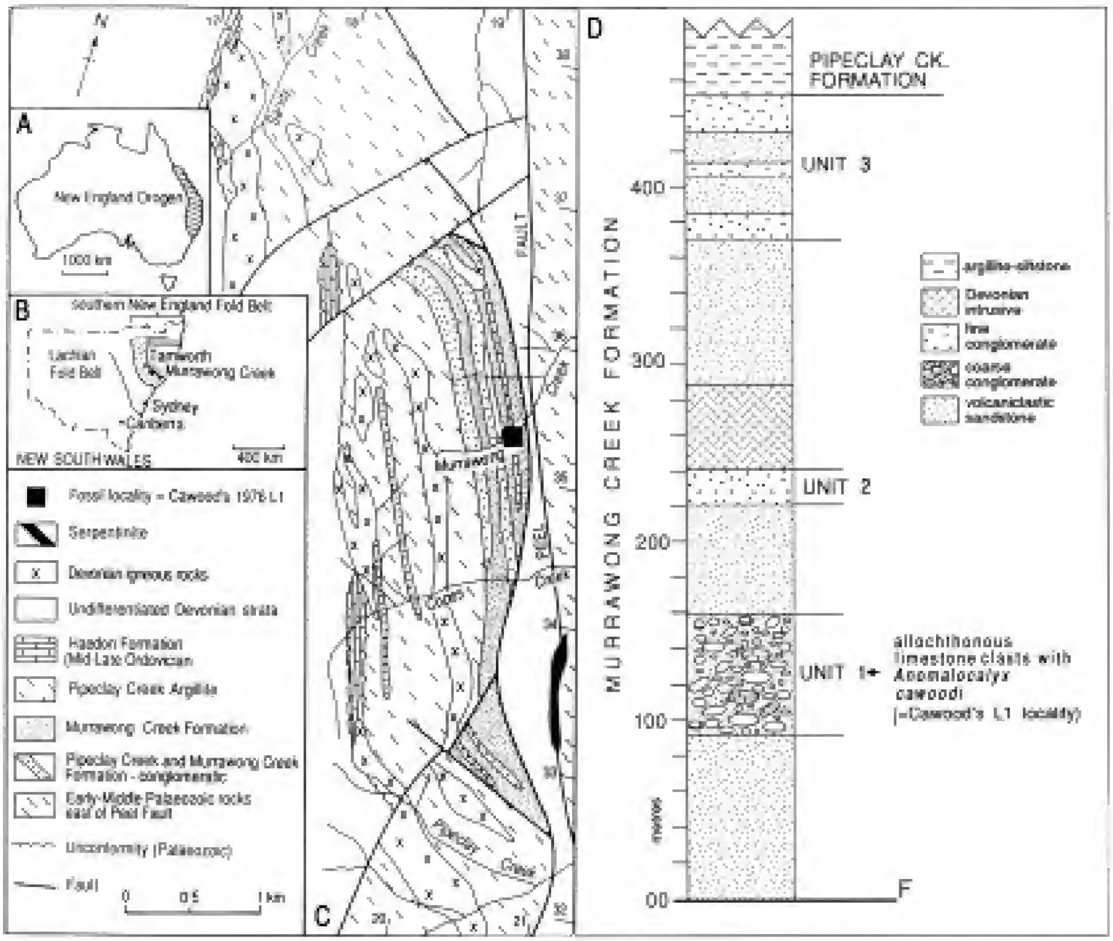

A
New England Orogen
1000 km
B
Southern New England Fold Belt
Lachlan Fold Belt
Tamworth
Murrawong Creek
Sydney
Canberra
NEW SOUTH WALES
400 km
Fossil locality = Cawood's 1976 L1
Serpentinite
Devonian igneous rocks
Undifferentiated Devonian strata
Haedon Formation (Mid Late Ordovician)
Pipeclay Creek Argillite
Murrawong Creek Formation
Pipeclay Creek and Murrawong Creek Formation - conglomeratic
Early-Middle Palaeozoic rocks east of Peel Fault
Unconformity (Palaeozoic)
Fault
0
0.5
1 km
N
C
Murrawong
Copes
Creek
FAULT
PEEL
Pipeclay Creek
D
PIPECLAY CK. FORMATION
UNIT 3
UNIT 2
UNIT 1
MURRAWONG CREEK FORMATION
400
300
200
100
00
F
argillite-siltstone
Devonian intrusive
fine conglomerate
coarse conglomerate
volcaniclastic sandstone
allochthonous limestone clasts with *Anomalocalyx cawoodi* (=Cawood's L1 locality)

Figure 1. A, generalised map of Australia showing extent of rocks associated with the New England Fold Belt. B, generalised map showing exposures of the southern New England Fold Belt and the locality of the Murrawong Creek area. C, geological map of the Murrawong Creek–Copes Creek area (modified after Leitch & Cawood [1987]). Black box depicts area where 21 allochthonous limestone clasts were re-collected in 1992 from Cawood's (1976) original L1 locality, Unit 1 in Murrawong Creek (grid reference: 198$_7$ 352$_4$, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°96'08"E). D, type section of the Murrawong Creek Formation, along Murrawong Creek, showing sampled conglomerate horizon, Unit 1 of Leitch & Cawood, 1987 (= Cawood's [1976] L1 locality). Modified after Leitch & Cawood, 1987, fig. 2.

Geological setting and age

The geology, stratigraphy and depositional environment of the Murrawong Creek Formation have been outlined in some detail by Brock (1998a,b), so only a summary is presented here. The Murrawong Creek Formation (Cawood, 1980) is the oldest of three lithostratigraphic units in the Copes Creek-Murrawong Creek region of the southern New England Fold Belt, with sporadic outcrops in a 4.5 km north–south trending tract of interbedded siltstone, sandstone and conglomerate, some 25 km south-southeast of Tamworth, 31°18'08"S 151°06'28"E (Fig. 1A–C; Cawood, 1976, 1980; Leitch *et al.*, 1988; Leitch & Cawood, 1996). The type section, along Murrawong Creek, consists of 450 metres of poorly outcropping, interbedded coarse to fine debris flow conglomerates, turbiditic sandstone, siltstone, siliceous mudstone and ash-fall tuffs (Fig. 1D). The base of the section is faulted against undifferentiated ?Devonian metasediments. Leitch & Cawood (1987, fig. 2) recognised three conglomerate horizons in the Murrawong Creek Formation, informally designated Units 1–3. Unit 1, the coarsest of the three units (Fig. 1D), includes 85 m of poorly outcropping, polymictic paraconglomerate with angular to subrounded, mostly volcanic, clasts (0.01–1.5 m in diameter) set in a poorly sorted sand to granule grade volcaniclastic matrix. The largest clasts are represented by fossiliferous limestones (Fig. 2).

Provenance investigations of the cobble and pebble sized igneous clasts from the Murrawong Creek Formation revealed that the clasts are from a low-K orogenic suite, and the absence of detritus characteristic of continental crust is consistent with an interpretation favouring derivation from an intra-oceanic island arc rather than a continental margin arc (Leitch & Cawood, 1987, 1996). The presence of small quantities of volcanic beta quartz fragments in the allochthonous limestone clasts also implies proximity to an island arc (Engelbretsen, 1996). The allochthonous volcaniclastic debris of the Murrawong Creek Formation and the conformably overlying Pipeclay Creek Formation were probably deposited as gravity flows in an inner submarine environment into relatively deep water conditions (Leitch & Cawood, 1987: 635) from an eroded western source (Leitch & Cawood, 1987; Leitch *et al.*, 1988). The faunal content of the limestone clasts includes diverse trilobite assemblages (Sloan, 1991), lingulate brachiopods (Engelbretsen, 1996), calciate brachiopods (Brock, 1998a), molluscs (Brock, 1998b) and an array of undescribed small shelly fossils that indicate the original setting for the fossiliferous carbonates was a relatively shallow-water carbonate platform, possibly fringing a volcanic island or islands.

The trilobite assemblage from the allochthonous limestone clasts (see Brock [1998a,b] for details of taxa) containing the new brachiopod *Anomalocalyx cawoodi*

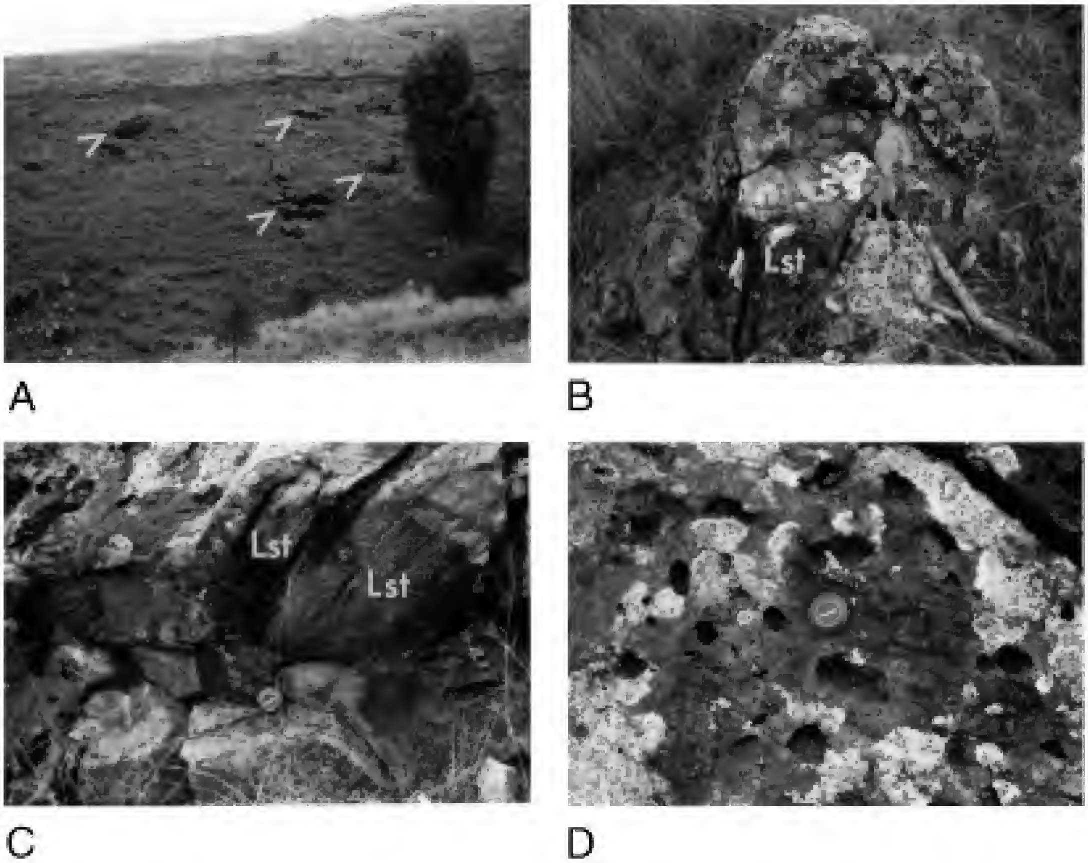


Figure 2. Field photographs of the Murrawong Creek Formation. A, wide angle shot, looking south, at some of the conglomeratic exposures of Unit 1 (arrowed); Murrawong Creek in foreground. B, lenticular, subrounded fossiliferous limestone clast (Lst), set in coarse volcaniclastic matrix of Unit 1. C, close-up of lenticular limestone clasts (Lst) in volcaniclastic matrix of Unit 1. D, weathered clast cavities in Unit 1 matrix. Lens cap 55 mm across in photographs B–D.

support an age spanning the *atavus–punctuosus* zones (Floran-Undillan Stages) using the Australian Middle Cambrian time-scale (Shergold, 1995).

Stewart (1995) reported the discovery of an assemblage of paraconodonts including *Muellerodus, Herzina, Prooneotodus* and *Furnishina*, and a number of minute forms similar to *Clavohamulus* and *Westergaardodina* from a dark, thinly bedded, spiculitic chert of the Pipeclay Creek Formation (Fig. 1D) in Copes Creek. The abundance of paraconodonts and the lack of euconodonts is consistent with a Middle Cambrian to early Late Cambrian age for this formation. It is thus clear that the Middle Cambrian allochthonous limestone clasts of the conformably underlying Murrawong Creek Formation are set in a matrix of similar age, as originally interpreted by Cawood (1976, 1980).

Preservation

All known specimens of *Anomalocalyx cawoodi* are preserved as epitaxial coatings of epidote. This type of preservation has previously been reported from the Murrawong Creek Formation in the coralomorph taxon *Tretocylichne perplexa* by Engelbretsen (1993: 55). A similar type of preservation, consisting of phosphatic epitaxial coatings, has also been described in the bivalve *Pojetaia runnegari* (Runnegar & Bentley, 1983) and the brachiopod-like taxon *Apistoconcha* (Bengtson *et al*., 1990: 171, fig. 113).

The epidote coating covers all inner and outer surfaces of *Anomalocalyx*, faithfully replicating elements of the external and internal morphology, including fine surface detail. The internal space between the inner and outer layers of the coating attests to an original calcareous shell composition subsequently dissolved during acetic acid processing. The presence of a calcareous shell in *Anomalocalyx* is supported by the fact that only taxa known to possess a calcareous shell (e.g., articulate brachiopods, *Nisusia* and *Arctohedra*, molluscs, chancelloriids, and hyolithids) are preserved in a similar manner.

The preservation of *Anomalocalyx* ranges from fine to very coarse, resulting in a wide variation of gross morphology, especially in shell outline, the shape of the coniform ventral valve, and the preservation of fine features of the external ornament.

Systematic palaeontology

All type specimens are held in the Australian Museum (AM); registration numbers are given below.

Phylum **Brachiopoda** Dumeril

Subphylum **?Rhynchonelliformea** Williams, Carlson, Brunton, Holmer & Popov, 1996

Class, Order, Superfamily, Family **Uncertain**

Anomalocalyx n.gen.

Type species. *Anomalocalyx cawoodi* n.sp.

Diagnosis. Minute, deeply coniform, tapering ventral valve with very high, variably convex to flattened, catacline to weakly procline, interarea; delthyrium narrow, covered for entire length by a well-developed, evenly convex pseudodeltidium. Radial costae low, wide, anteriorly bifurcating, becoming fluted at commissural margin. Costae crossed at more or less regular intervals (70–100 µm) by low, undulose concentric growth lamellae. Valve outline variably subquadrate to subhexagonal. Teeth simple, rounded, dorsally directed, nub-like projections situated on the posterior valve wall either side of the delthyrium; an elongate, tapering, tube-like structure extends ventrally along the entire length of the delthyrial cavity directly under the convex pseudodeltidium. Dorsal valve with well-developed incurved umbo, broad median sulcus and anterior tongue. Interior with small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Notothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Discussion. *Anomalocalyx* displays a number of features indicative of a brachiopod assignment. These include, (*a*) a bivalved shell with the plane of bilateral symmetry bisecting the midline of both valves, (*b*) a pair of simple dorsally directed, nub-like teeth projecting from the posterior shell wall of the ventral valve, (*c*) a high, flattened ventral interarea bisected medianly by an elongate delthyrium covered by a prominent, arched pseudodeltidium, (*d*) well defined radial costae, crossed at more or less regular intervals by continuous concentric growth lamellae, (*e*) a convex dorsal valve with simple socket plates, and (*f*) an inferred calcium carbonate shell composition. The presence of a calcareous shell composition, simple teeth in the ventral valve with an arched pseudodeltidium covering the delthyrium and dorsal sockets either side of a wide notothyrial gap conforms, at least partly, with the concept of the subphylum Rhynchonelliformea as outlined by Williams *et al.* (1996: 1192). *Anomalocalyx* is therefore referred, with some hesitation, to the Rhynchonelliformea.

The lack of information regarding muscle scars, mantle canal pattern and nature of the ventral umbo in *Anomalocalyx* precludes confident assignment to higher taxonomic levels within the Brachiopoda at the present time. The presence of a well-developed, convex pseudodeltidium flanked by flattened propareas in the ventral valve and a wide, triangular, open notothyrium (lacking a cardinal process) bordered by socket plates in the dorsal valve indicates *Anomalocalyx* may have some relationship to the order Kutorginida (Popov *et al*., 1997). However, kutorginids are characterised by a large posterior median opening that is interpreted to have been the opening of a posteromedianly directed anus. The highly incurved dorsal valve and the nature of the articulation of the valves indicates no such opening existed in *Anomalocalyx* (Fig. 3C). Though some kutorginids, such as *Nisusia alaica* (Popov &

Tikhonov, 1990, pl. 3, fig. 23), possess moderately coniform ventral valves, none have the exaggerated form of *Anomalocalyx*, nor has any been described with an interior tube.

The elongate, irregular, tapering conical shape of the ventral valve of *Anomalocalyx* (Figs. 3C, 4A–L), though unusual amongst Cambrian calciate brachiopod orders, can be found in a few highly specialised, aberrant post-Cambrian taxa, such as the Silurian triplesiid *Onychotreta* Ulrich & Cooper (see Amsden, 1968), the highly specialised cemented ventral valves of the Permian richthofenioid brachiopods *Cyclacantharia* and *Sacchinella* (see Cooper & Grant, 1975), and the Permian nasute (coralliform) gemmellaroid genera *Cyndalia* and *Gemmellaroia* (Grant, 1993). *Cyndalia*, in particularly, displays a remarkable number of features similar to *Anomalocalyx*. Both taxa are micromorphic with calcium carbonate shells, and possess an elongate, tapering ventral valve (extravagant in *Cyndalia*) with well-developed pseudodeltidium. Though a short pedicle tube is present in species of the obolellid genus *Trematobolus* (Geyer & Mergl, 1995), the elongate tube-like structure situated directly under the arched pseudodeltidium and extending along the entire ventral wall of the ventral valve in *Anomalocalyx* has not previously been described in a Cambrian articulate brachiopod. Geyer & Mergl (1995) suggested the tube in *Trematobolus* probably housed a specialised pedicle similar to that found in *Discinisca*. The function of this tube in *Anomalocalyx* remains enigmatic, but it shows a remarkable similarity to the elongate, tapering tube-shaped structure in *Cyndalia* (see Grant, 1993, fig. 6) described as a tube-like spondylium produced by the coalescence of dental plates and a median septum, suggesting they formed a moving muscle attachment area (Grant, 1993: 55). The lateral margins of the tube-like structure in *Anomalocalyx* appear as though they are attached either side of the delthyrium, directly under the dorsally directed nub-like teeth (Figs. 3B, 4A,J–K,M), as would be expected if the structure were a spondylium for muscle attachment (Fig. 3C). If a spondylium interpretation is accepted, the function of the u-shaped groove on the outer surface of the spondylial tube (Figs. 3B, 4J) remains enigmatic. The fact that all ventral valves of *Anomalocalyx* have a broken apex makes it difficult to determine the presence or absence of an apical pedicle foramen. It seems unlikely that the tube actually housed a pedicle given the extraordinary length of the tube inside the ventral valve.

Close affinity between *Anomalocalyx* and *Cyndalia* is unlikely given their disjunct stratigraphic positions. The degree of morphological similarity between these two taxa may well be the result of convergent evolution, reflecting an analogous evolutionary response to specialised environmental circumstances. The ecology of both taxa is imperfectly known, but Grant (1993: 59) envisaged *Cyndalia* inhabiting a turbid, muddy, shallow water, lagoonal setting. Given the allochthonous setting of the *Anomalocalyx*-bearing clasts, the original environmental setting is even more difficult to reconstruct, but contemporaneous faunal assemblages suggest *Anomalocalyx*

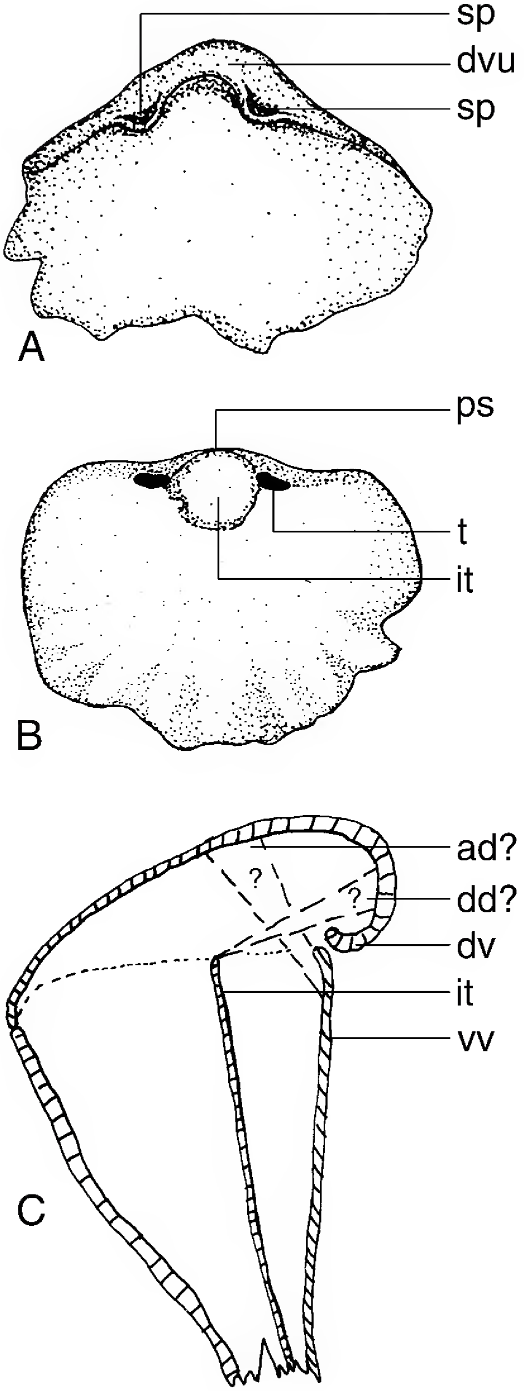


Figure 3. A, dorsal valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on AM F107869; valve width 1 mm. B, ventral valve interior of *Anomalocalyx cawoodi* n.gen. et n.sp., based on numerous specimens; valve width approximately 1.5 mm. C, tentative reconstruction along axial longitudinal plane of conjoined specimen of *Anomalocalyx cawoodi* n.gen. et n.sp. showing speculative position of adductor and diductor muscles. The interior tube in the ventral valve is reconstructed as a spondylial platform. Abbreviations: ad?, speculative adductor muscle; dd?, speculative diductor muscle; dv and dvu, dorsal valve and dorsal valve umbo; it, interior (spondylial) tube; ps, pseudodeltidium; sp, socket plates; t, tooth; vv, ventral valve.

was probably associated with a shallow water carbonate platform fringing a volcanic island arc (Brock, 1998a,b). The elongate ventral valves of both taxa are similar to those found in some rudist bivalves, and are best explained as an adaptation for keeping the aperture elevated above the muddy substrate (Grant, 1993: 59). However, because of the millimetric dimensions of the shell, an infaunal, epifaunally attached, or cryptic life habit cannot be completely ruled out.

The possibility that *Anomalocalyx* may represent a new type of coral-like organism similar to *Tretocylichne* Engelbretsen, 1993 or the operculate *Cothonion* Jell & Jell, 1976 cannot be completely ruled out. However, close comparison of these two unusual forms reveals that *Anomalocalyx* lacks the octagonal outline, longitudinal septa on the inner surface of the calyx, perforate expanded base, and thecal budding characteristic of *Tretocylichne* Engelbretsen, 1993. The slightly older operculate genus, *Cothonion* described by Jell & Jell (1976) from the early Middle Cambrian Coonigan Formation, western New South Wales has a similar shape to the putative ventral valve of *Anomalocalyx*, but *Cothonion* can be discriminated by the presence of strong internal septa, and the operculum is generally flattened or upturned (concave) at the midpoint, and internally, is characterised by the development of strong radial septa. No coralomorph taxon yet described has been discovered with the brachiopod-like teeth or the interior tube characteristic of *Anomalocalyx*.

Etymology. The Greek word *anomalos* for unusual, abnormal, deviating from the general rule is combined with *kalyx* (Greek) for cup.

Anomalocalyx cawoodi n.sp.

Figs. 3A–C, 4A–P

Type material. HOLOTYPE: ventral valve from clast W10, AM F97383, Fig. 4A–E. PARATYPES 11 ventral valves (VV hereafter) and 22 dorsal valves (DV hereafter) as follows: 3 VV, AM F97384 (Fig. 4F–I), AM F107867 (Fig. 4J–L) and AM F97385 (Fig. 4M); 3 DV, AM F107868 (Fig. 4N), AM F107869 (Fig. 4O) and AM F107870 (Fig. 4P); 6 DV, AM F112571–76, and 2 VV, AM F112577–78, from clast W1; 3 DV, AM F112579–81, from clast W3; 2 DV, AM F112582–83, and 2 VV, AM F112584–85, from clast W10; 2 DV, AM F112586–87, and 1 VV, AM F112588, from clast W38; 6 DV, AM F112589–94, and 3 VV, AM F112595–97, from clast W/L1/S4.

Type locality. Allochthonous limestone clasts, Unit 1, Murrawong Creek Formation. Equivalent to Cawood's (1976) original L1 locality (Fig. 1C). Grid Reference: 198_7 352_4, Woolomin 1:25,000 topographic sheet 9135-111-N, 31°18'08"S 151°06'28"E.

Diagnosis. As for genus.

Description. Shell minute (maximum width 2 mm, maximum length 1.8 mm), with variable shell outline ranging from semicircular to subquadrate to subhexagonal. Maximum shell width approximately midvalve. External ornament consists of between 10–14 low, wide (0.2–0.3 mm), rounded costae increasing anteriorly by bifurcation, becoming fluted at the commissure. Intercostal furrows wide and shallow. Costellation and intercostal regions crossed by a series of continuous, low and undulose concentric growth lamellae spaced at intervals of approximately 0.1 mm.

Ventral valve deep, curved, irregularly conical, tapering apically, with high (max. 3.0 mm), variably developed, catacline to weakly procline interarea. Interareas flattened to weakly convex; barely perceptible in some specimens as they merge and arch medianly forming a single convex pseudodeltidium. Concentric lamellae cross interareas and pseudodeltidium. All known ventral valves broken, so apical morphology (including presence or absence of a foramen) unknown. Interior of ventral valve with an elongate, tapering tube-like structure (maximum width 0.6 mm) extending ventrally along the entire delthyrial cavity directly under the pseudodeltidium. A u-shaped groove (0.15 mm wide), narrowing gradually with the ventral direction of valve taper, present on anterolateral surface of tube. Short, stubby, dorsoventrally flattened, convergent teeth arise as simple, dorsoanteriorly directed projections from posterior shell wall in most specimens. Muscle scars not preserved.

Putative dorsal valve strongly convex, with short, curved hingeline and broad, shallow, anteriorly widening, median sulcus. Umbo enlarged and recurved, almost forming a hood over the notothyrium. External ornament similar to ventral valve, though radial costae tend to arise via implantation rather than bifurcation. Small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall. Nothothyrium wide, but poorly defined; other cardinal features absent. Musculature and vascular markings in both valves unknown.

Remarks. Though no articulated specimens of *A. cawoodi* have been recovered, a number of convex valves of appropriate size, with similar outline and ornament to the ventral valve have been identified as matching dorsal valves (Figs. 3A, 4N–P). Internally, the cardinal area of the putative dorsal valve is very simple, with a wide notothyrium bordered by simple socket-like plates excavated into the posterior shell wall (Figs. 3A, 4N–O). Multiple epitaxial coatings of these valves is sometimes so thick that the socket plates become extravagantly enlarged, making the edges of the socket-plates project forward like teeth, mimicking the morphology of a simple ventral valve. Inspection of paratypic dorsal valves without multiple coatings of epidote display an unmistakable, but simple, dorsal valve morphology (Figs. 3A, 4N–O). The articulatory mechanism in *A. cawoodi* was clearly very rudimentary. The simple, rounded, nub-like teeth must have slotted into the matching sockets excavated in the posterior shell wall of the dorsal valve. There is no evidence of a cardinal process. The dorsal valve has an unusually enlarged, incurved umbo, almost forming a notothyrial hood, and this may have been the site for direct muscle attachment (Fig. 3C). A consequence of the enlarged dorsal umbo is that, when articulated, a restricted valve gape must have resulted, and there would

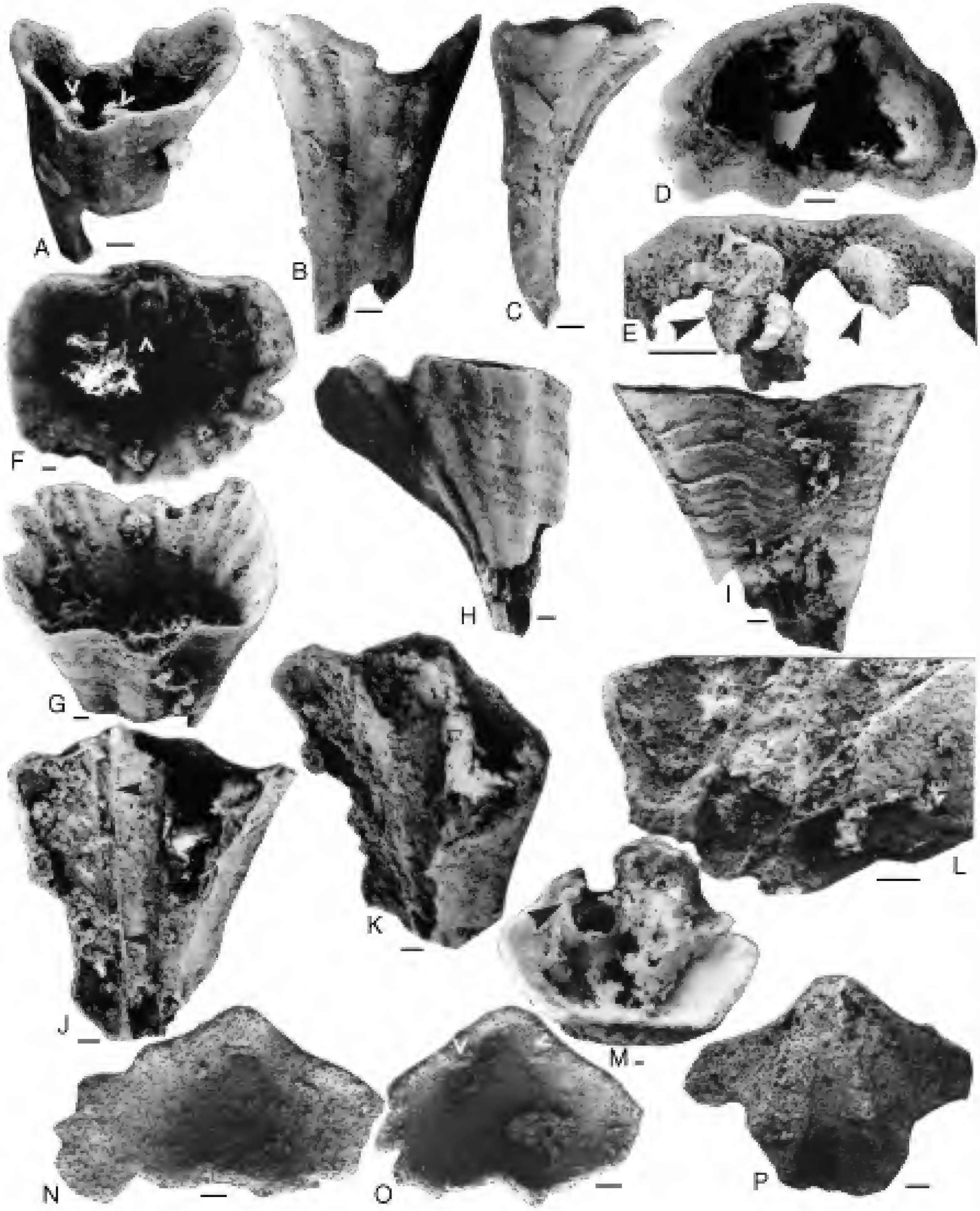


Figure 4. A–P, *Anomalocalyx cawoodi* n.gen. et n.sp. A–E, AM F97383, holotype from clast W10: A, oblique posterior view of holotype ventral valve showing teeth (arrowed); B, anterior view showing sulcate commissure; C, lateral view showing elongate, curved and tapering ventral valve; D, interior view; E, close-up of teeth (arrowed) in holotype. F–I, AM F97384, paratype ventral valve from clast W10: F, oblique interior showing interior tube (arrowed) with teeth broken away in specimen; G, oblique posterior view showing well-developed interarea and arched pseudodeltidium; H, lateral view; I posterior view showing undulose concentric growth lines. J–L, AM F107867, broken paratype ventral valve from clast W1: J, broken interior of ventral valve showing tapering interior (spondylial) tube with u-shaped external groove (arrowed); K, oblique view showing interior tube; L, close up of posterior portion of interior tube (infilled with sediment). M, AM F97385, paratype ventral valve from clast W10, showing dorsal portion of interior tube and a nub-like tooth (arrowed). N, AM F107868, interior of abraded paratype dorsal valve from clast W1 showing wide notothyrial gap. O, AM F107869, interior of abraded paratype dorsal valve from clast W1 showing simple socket plates (arrowed). P, AM F107870, exterior of abraded paratype dorsal valve from clast W1 showing anterior tongue. All scale bars 100 µm.

have been no posterior gap between the posterior edge of the pseudodeltidium and the dorsal umbo for a pedicle opening.

Etymology. In honour of Dr Peter Cawood, who discriminated and named the Murrawong Creek Formation and was the first to discover Cambrian fossils in this formation.

ACKNOWLEDGMENTS. Earlier drafts of this manuscript were considerably improved by comments and suggestions by A. Boucot (Oregon), F. Alvarez (Oviedo), N. Archbold (Melbourne), G. Wilson (Sydney), and A. Simpson (Sydney). Constructive reviews were provided by Lars Holmer (Uppsala) and Leonid Popov (Cardiff). Thanks to T. Sloan, who took the field photographs and M. Engelbretsen for assistance with scanning electron microscopy; D. Mathieson (MUCEP) helped with photographic printing. Partial funding for this work was provided by a 1999 Small ARC Grant.

References

Aksarina, N.A., & Yu.L. Pelman, 1978. Kembriyskiye brakiopody i dvustvorchatyye millyuski Sibiri. *Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie, AN SSSR*, 362. [In Russian].

Amsden, T.W., 1968. Articulate Brachiopods of the St. Clair Limestone (Silurian), Arkansas, and the Clarita Formation (Silurian), Oklahoma. *Paleontological Society Memoir* 1: 1–117.

Bengtson, S., S. Conway Morris, B.J. Cooper, P.A. Jell & B.N. Runnegar, 1990. Early Cambrian fossils from South Australia. *Memoir of the Association of Australasian Palaeontologists* 9: 1–364.

Brock, G.A., 1998a. Middle Cambrian articulate brachiopods from the southern New England Fold belt, eastern Australia. *Journal of Paleontology* 72: 604–618.

Brock, G.A., 1998b. Middle Cambrian molluscs from the southern New England Fold Belt, northeastern N.S.W. *Geobios* 31: 571–586.

Cavalier-Smith, T., 1998. A revised six-kingdom system of life. *Biological Reviews* 73: 203–266.

Cawood, P.A., 1976. Cambro-Ordovician strata, northern New South Wales. *Search* 7: 378–379.

Cawood, P.A., 1980. *The geological development of the New England Fold Belt*. Unpublished Ph.D. Thesis, The University of Sydney, pp. 429.

Cooper, G.A., & R.E. Grant, 1975. Permian brachiopods of West Texas, III. *Smithsonian Contributions to Paleobiology* 19: 1–1298.

Engelbretsen, M.E., 1993. A Middle Cambrian possible cnidarian from the Murrawong Creek Formation, NE New South Wales. *Memoir of the Association of Australasian Palaeontologists* 15: 51–56.

Engelbretsen, M.E., 1996. Middle Cambrian lingulates from the Murrawong Creek Formation, north eastern New South Wales. *Historical Biology* 11: 69–99.

Geyer, G., & M. Mergl, 1995. Mediterranean representatives of the obolellid *Trematobolus* Matthew (Brachiopoda) and a review of the genus. *Paläontologische Zeitschrift* 69: 181–211.

Grant, R.E., 1993. The brachiopod family Gemmellaroiidae. *Journal of Paleontology* 67(1): 53–60.

Jell, J.S., & P.A. Jell, 1976. Early Middle Cambrian corals from western New South Wales. *Alcheringa* 1: 181–195.

Leitch, E.C., M. Iwasaki, H. Honma, T. Watanabe, S. Iizumi, H. Ishiga & Y. Kawachi, 1988. The structure of the southern part of the New England Fold Belt. In *Preliminary Report on the Geology of the New England Fold Belt*, pp. 9–31. Australia, vol. 1, pp. 237.

Leitch, E.C., & P.A. Cawood, 1987. Provenance determination of volcaniclastic rocks: the nature and tectonic significance of a Cambrian conglomerate from the New England Fold Belt, eastern Australia. *Journal of Sedimentary Petrology* 57(4): 630–638.

Leitch, E.C., & P.A. Cawood, 1996. Early Palaeozoic convergent margin elements in the New England Fold Belt and the inception of the Pacific ring of fire. 13th Australian Geological Convention, Canberra. *Geological Society of Australia, Abstracts* 41: 246.

Lui Di-Yong, 1979. Earliest Cambrian brachiopods from South West China. *Acta Palaeontologia Sinica* 18: 505–511. [In Chinese with English summary].

Parkhaev, P.Yu., 1998. Siphonoconcha—a new class of Early Cambrian bivalved organisms. *Paleontological Journal* 32(1): 1–15.

Popov, L.Ye., 1992. The Cambrian radiation of brachiopods. In *Origin and early evolution of the Metazoa*, ed. P.W. Signor, pp. 399–423. New York, Plenum Press.

Popov, L.E., L.E. Holmer & M.G. Bassett, 1996. Radiation of the earliest calcareous brachiopods. In *Abstracts from the Third International Brachiopod Congress*, eds. P. Copper & J. Jin, pp. 209–213. Laurentian University, Sudbury, Canada.

Popov, L.E., L.E. Holmer, A.J. Rowell & J.S. Peel, 1997. Early Cambrian brachiopods from North Greenland. *Palaeontology* 40(2): 337–354.

Popov, L.E., & A.Yu. Tikhonov, 1990. Early Cambrian brachiopods from Southern Kirgizia. *Paleontologicheskii zhurnal* 1990: 33–45.

Roberts, J., & P.A. Jell, 1990. Early Middle Cambrian (Ordian) brachiopods of the Coonigan Formation, western New South Wales. *Alcheringa* 14: 257–309.

Runnegar, B.N., & C. Bentley, 1983. Anatomy, ecology and affinities of the Australian early Cambrian bivalve *Pojetaia runnegari* Jell. *Journal of Palaeontology* 57: 73–92.

Shergold, J.H., 1995. Timescales 1, Cambrian. *AGSO Record* 1995/30, pp. 32.

Sloan, T.R., 1991. *Late Middle Cambrian Trilobites from Allochthonous Blocks in the Murrawong Creek Formation, N.S.W.* Unpublished M.Sc. Thesis. Macquarie University, Sydney, pp. 74 + appendix.

Stewart, I., 1995. Cambrian age for the Pipeclay Creek Formation, Tamworth Belt, northern New South Wales. *Courier Forschungsinstitut Senckenberg* 82: 487.

Williams, A., S.J. Carlson, C.H.C. Brunton, L.E. Holmer & L.E. Popov, 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London, series B* 351: 1171–1193.

Manuscript received 19 April 1999, revised 25 June 1999 and accepted 12 July 1999.

Associate Editor: G.D. Edgecombe.

© Copyright Australian Museum, 1999
Records of the Australian Museum (1999) Vol. 51: 187–214. ISSN 0067-1975

Systematics, Biostratigraphy and Evolution of the Late Ludlow and Přídolí (Late Silurian) Graptolites of the Yass District, New South Wales, Australia

R.B. RICKARDS[1] AND A.J. WRIGHT[2]

[1] Department of Earth Sciences, University of Cambridge, England
wagreen@esc.cam.ac.uk

[2] School of Geosciences, University of Wollongong, Wollongong NSW 2522, Australia
tony_wright@uow.edu.au

ABSTRACT. Graptolites from the Yass district of New South Wales include important material from: low in the Black Bog Shale; from the Yarwood Siltstone Member; 2 levels high in the Black Bog Shale; 2 levels low in the Rosebank Shale; low in the Cowridge Siltstone; and in the lower part of the Elmside Formation. The faunas from the lower 4 levels are late Ludlow (early Late Silurian), and the higher 4 levels are Přídolí (late Late Silurian).

Twenty-seven graptolite taxa, a considerable increase on previous records from Yass, have been identified in the late Ludlow and Přídolí of the district. These taxa enable the Ludlow-Přídolí boundary to be identified some 20 m above the base of the Rosebank Shale (Booroo Ponds Group); our stratigraphically highest collection from the Elmside Formation is latest Přídolí, supporting the previous placement of the base of the Devonian approximately midway through the Elmside Formation (Barambogie Group). The following graptolite Biozones have been identified: *praecornutus, cornutus, parultimus, bouceki* and *transgrediens*. Twenty Yass taxa are described, including the new species *Bohemograptus paracornutus, Pristiograptus shearsbyi, Neocucullograptus? yassensis* and *N.? mitchelli* and the new subspecies *Monograptus perneri elmsidensis* and *M. formosus jenkinsi*. The following are recorded from Australia for the first time: *Bohemograptus praecornutus* Urbanek, 1970; *Crinitograptus operculatus* Münch, 1938; and *Pristiograptus kolednikensis* Přibyl, 1940. *Dictyonema* sp. cf. *D. sherrardae* Rickards *et al.*, 1995 and *D. elegans* Bulman, 1928 are considered late evolutionary derivatives of long-ranging dendroid species. *Linograptus posthumus introversus* Rickards & Wright, 1997 is interpreted as a short-lived, late Ludlow offshoot of the long-ranging *L. p. posthumus* Richter, 1875. *Bohemograptus praecornutus* is regarded as the ancestor of *B. paracornutus*, the *B. cornutus* evolutionary plexus being recognised for the first time in Australia. Late forms of *Pristiograptus dubius* (Suess, 1851) probably gave rise to *P. shearsbyi* n.sp. and *Pristiograptus kolednikensis* probably arose in the basal Přídolí from the late Ludlow *P. fragmentalis* (Bouček, 1936). Some material described and discussed by Brown & Sherrard (1952) is reinterpreted.

Bohemograptus paratenuis n.sp. is proposed for material assigned by Urbanek (1970) to *B. bohemicus* aff. *tenuis* (Bouček, 1936); this species is known only from Poland.

RICKARDS, R.B., & A.J. WRIGHT, 1999. Systematics, biostratigraphy and evolution of the late Ludlow and Přídolí (Late Silurian) graptolites of the Yass district, New South Wales, Australia. *Records of the Australian Museum* 51(3): 187–214.

The Yass Silurian sequence of New South Wales has been recognised as one of the most important developments of the system in Australia (Jell & Talent, 1989). Among the fossil groups abundantly represented in the Yass strata, conodonts and graptolites are the most important for determining the age relationships of the strata; the conodont faunas were described by Link & Druce (1972) but the graptolites have been, by comparison, poorly known. In this paper we identify the graptolite faunas from a number of stratigraphic levels in the Yass sequence, and determine the ages and evolutionary relationships of the faunas.

The early explorer-geologist Strzelecki (1845) was the first to note the occurrence in the Yass district of strata we now recognise as Silurian. Graptolites from the Yass Silurian were first noted by the local schoolteacher, John Mitchell (1886, 1888: from "Bowning Beds, Bowning" and "Bell [sic] Vale"). The first brief graptolite description (as "allied to *M. dubius*") and illustration were by T.S. Hall (1903: Bowning Series, Belle Vale). Although "Belle Vale" is still a well-known property on the Black Range Road in the Yass district (Fig. 1), these reports are of historic interest only as the locality and material are not recognisable from published data. A.J. Shearsby, a local photographer and keen amateur geologist, noted in 1912 the graptolites *Monograptus* (?) and *Dendrograptus* from strata identified by him as the "Barrandella shales".

The stratigraphic terminology for the Silurian strata of the area has evolved considerably from the pioneering descriptions by Shearsby (1912) and Brown (1941), to the current stratigraphic terminology proposed by Link (1970), followed by Link & Druce (1972) in their seminal studies of conodonts from the Yass Silurian, and finally modified by Cramsie *et al.* (1978).

Sherrard & Keble (1937) described Ordovician and Silurian graptolites from the Yass area. Surprisingly (in view of the abundant graptolites at other levels in the Yass Silurian sequence) the Silurian graptolites they described were Přídolí forms from near "Silverdale" NNW of Yass (Fig. 1), under the names of *Monograptus flemingii* (Salter), *M.*

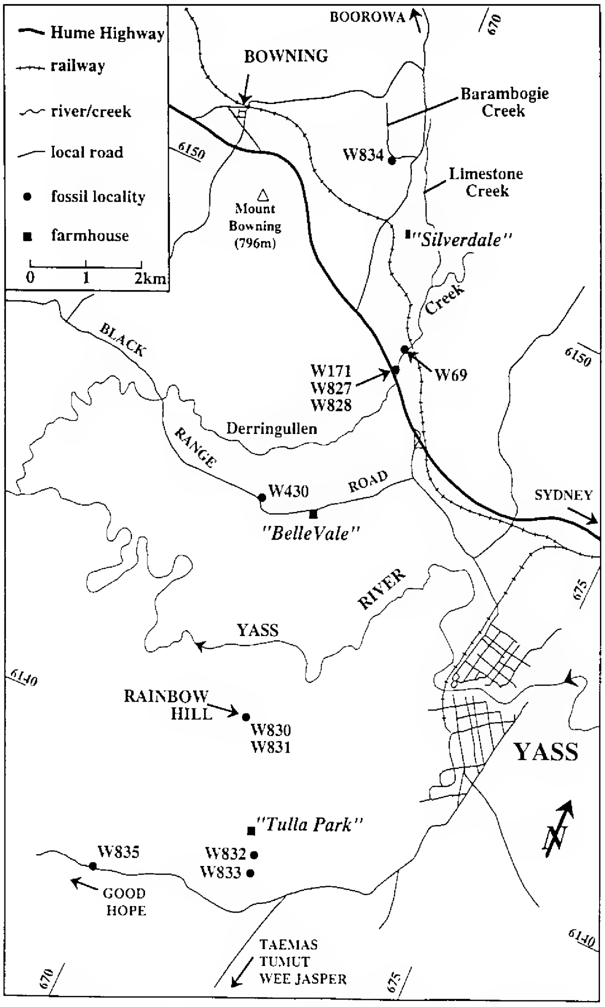


Figure 1. Locality map for the Yass district. Geological details can be obtained from Link & Druce (1972). The 3 and 4 digit numbers adjacent to short lines along the figure margins indicate the metric grid for the Yass 8628-S 50 000 map sheet.

Table 1. A comparison of previously identified graptolites from the Yass district, and present identifications of Yass graptolites.

Sherrard & Keble, 1937	Brown & Sherrard, 1952	Jaeger, 1967	Packham, 1968	this paper
	M. bohemicus	*M. bohemicus* subsp. B		*Bohemograptus paracornutus* n.sp.
M. cf. *nilssoni*	*M. nilssoni*	*Linograptus p. posthumus*		*L. p. posthumus* *L. p. introversus*
	M. roemeri	*M. bohemicus*		*B. paracornutus* n.sp.
	M. crinitus	*M. scanicus* group		?*L. p. posthumus*
M. cf. *tumescens*		*M. dubius* group	*M.* cf. *ultimus*	*M. parultimus*
M. flemingii	*M. salweyi*	*M. bouceki*		*M. bouceki*
M. cf. *vomerinus*		*M. transgrediens*		*M. transgrediens*
M. cf. *nilssoni*				
		M. bohemicus subsp. A		*B. praecornutus*
		M. formosus	*M. formosus*	*M. formosus*

cf. *tumescens* Wood, *M.* cf. *vomerinus* (Nicholson), *M.* sp. cf. *M. nilssoni* (Barrande) and *Dictyonema* sp.

A more significant step in the study of the graptolites of the Yass district was made by Brown & Sherrard (1952), who first drew attention to the existence of what has traditionally been known as the "*Monograptus bohemicus*" fauna at Yass. Subsequent work on this "*bohemicus*" fauna (now best known from Rainbow Hill) has been limited to a few preliminary comments by Jaeger (1967), which are discussed as appropriate in the taxonomic section of this paper. Brown & Sherrard described this "*bohemicus*" fauna under the names of *Monograptus bohemicus* Barrande, 1850, *M. nilssoni, M. crinitus* Wood, *M. roemeri* (Barrande) and *Dictyonema* sp. We have restudied their illustrated "*bohemicus*" material and conclude that it is (1) not *B. b. bohemicus* but *B. b. tenuis* (Bouček, 1936), and (2) possibly is not from Rainbow Hill but from exposures of a slightly different level (B, probably just below our level 2: see Fig. 2) high in the Black Bog Shale, possibly along strike towards the Yass River (Fig. 1). Some of Brown & Sherrard's illustrated graptolites are re-illustrated in Fig. 11 and re-identified in Table 1 herein. Brown & Sherrard also restudied the "Silverdale" fauna, from which they determined and described *Monograptus salweyi* (Hopkinson), *M.* sp. cf. *M. tumescens* Wood and *Dictyonema*.

Both Jaeger (1967) and Packham (1968) studied graptolites from levels other than those studied by Brown & Sherrard (1952). Packham identified *Monograptus formosus* Bouček, 1931b and *Monograptus* cf. *M. ultimus* Perner, 1899 from the Rosebank Shale at the junction of the (then) Hume Highway and Derringullen Creek, above the unit now known as the Rainbow Hill Marl Member of the Rosebank Shale (Link & Druce, 1972), and considered this fauna basal Přídolí, with which we concur.

Jaeger (1967) commented briefly on graptolites from three levels in the Yass sequence. Firstly, he studied the graptolite fauna previously studied by Sherrard & Keble (1937) from the lower part of the Cowridge Siltstone at the locality known as "Silverdale" (Fig. 1), which is close to our locality W834. He showed that these former workers had incorrectly identified *Monograptus bouceki* Přibyl, 1940 as *Monograptus salweyi* from this locality; he also recorded *Monograptus transgrediens* Perner, 1899 from his "Silverdale" material, and considered the fauna to be Přídolí. Secondly, he identified *Monograptus formosus* and "*M.* sp. of the *M. dubius* group" from Packham's (1968) locality, and the latter also from the locality near the Good Hope road (see Brown & Sherrard, 1952, fig. 1). Thirdly, he made interesting preliminary comments on the bohemograptids from below the Rainbow Hill Marl, from an unspecified locality. With regard to his collections from Yass (and Quarry Creek, cited by Jaeger, 1991), recent information suggests that these collections may be in the Humboldt Museum in Berlin.

The most recent advance in the study of Yass Silurian graptolites was by Jenkins (1982) who described a latest Přídolí fauna from the lower part of the Elmside Formation. Some Elmside material illustrated by Jenkins (1982) is refigured here in Fig. 12.

Despite the above record of graptolite research, the Yass sequence of Silurian graptolites has remained poorly known by world standards; in particular, the supposed "*Monograptus bohemicus*" fauna from the topmost beds of the Black Bog Shale has remained essentially unstudied for almost 45 years.

Our stratigraphically lowest specimens are from the Black Bog Shale, although Shearsby (1912), Jaeger (1967) and Cramsie *et al.* (1978) reported material from lower in the sequence. We have made new graptolite collections from most of the important localities mentioned by the above workers, as well as other localities, and now have 27 graptolite taxa from the area, spanning the Ludlow-Přídolí interval. This work has significantly extended the faunal diversity previously noted from most localities; some newly recorded taxa are surprisingly common in our collections.

Materials and method

Material cited and figured in this study is deposited in the Australian Museum; a supplementary collection is held for comparative purposes in the Sedgwick Museum, Department of Earth Sciences, University of Cambridge. "AMF" are Australian Museum numbers and "SM X." are Sedgwick Museum. Material reported by Jaeger (1967) has not been available for study, but it may be in the Humboldt Museum für Naturkunde, Berlin. However, with the exception of *Monograptus formosus* we have ample duplicate collections. Most taxa plotted on Fig. 2 are here both illustrated and described, but a few are merely illustrated. Elmside Formation specimens described by Jenkins (1982) have not been redescribed here, except for *M. formosus jenkinsi* n.subsp. (=*M. formosus* of Jenkins), *M. transgrediens* and *M. hornyi* (=*M.* cf. *angustidens* of Jenkins).

The graptolites are preserved in a variety of rock types from fine mudrock and shale to medium sandstones. Often they are in full relief. There is some slight tectonic deformation at some localities, and is indicated as appropriate on the illustrations; not all specimens from any one locality appear to be affected in the same way. There is some soft sediment deformation, especially of more slender species. However, in general the material is excellently preserved and more or less undeformed. The taxonomy is that recently used by Rickards *et al.* (1995), Rickards & Wright (1997) and Koren′ & Sujarkova (1997). Measurements of thecal spacing are given in the manner devised by Packham (1962), which we prefer to Howe's (1983) 2TRD technique: the latter we find less readable and more difficult to compare quickly with older methods of measurement. Σ is the distance from the sicular aperture to the most distal extremity of the first theca.

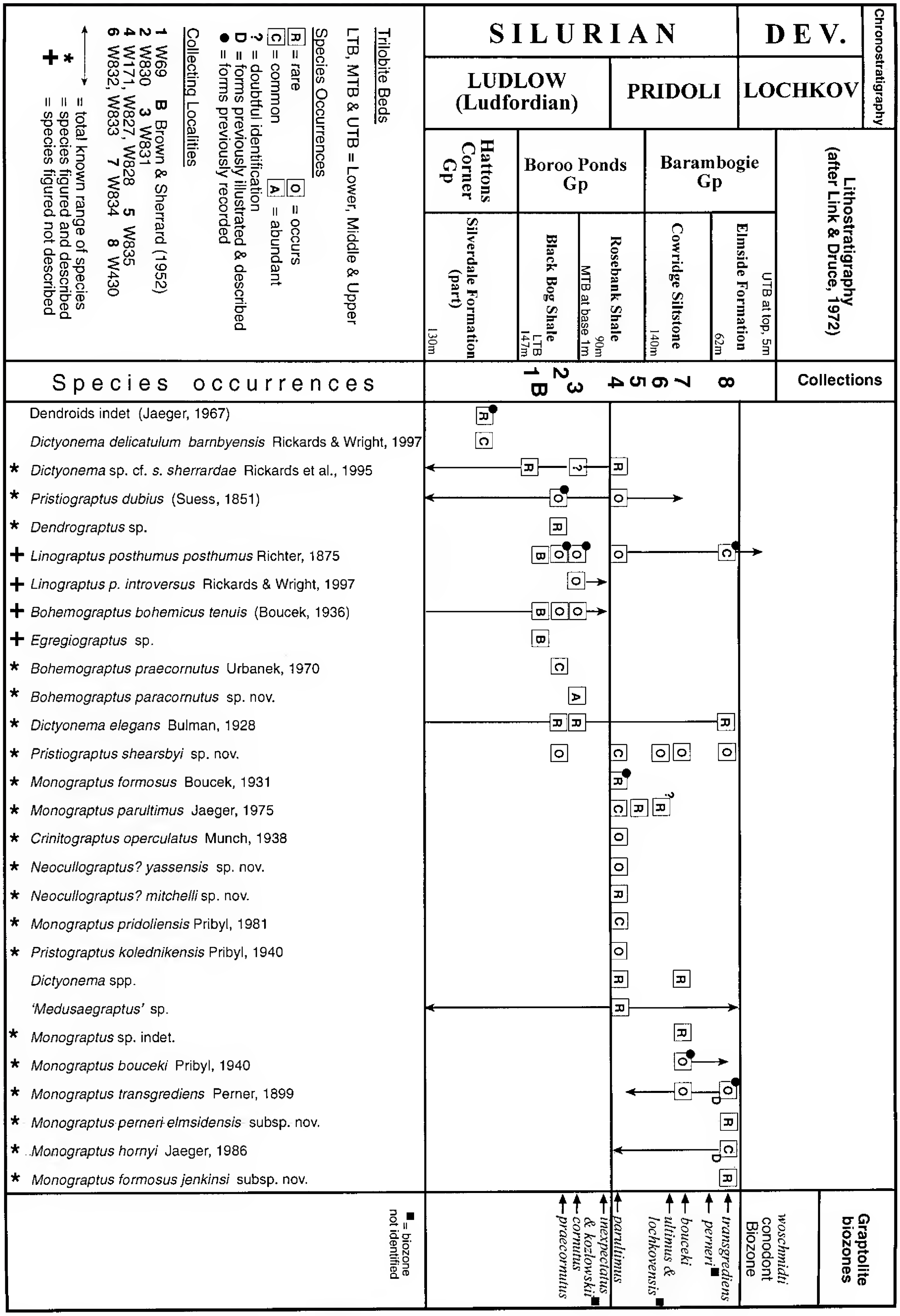


Figure 2. Ranges of identified graptolites plotted against lithostratigraphy and proposed biostratigraphy and chronostratigraphy. Elmside Formation occurrences are partly after Jenkins (1982). The symbols indicating numbers of specimens are approximately: R, 1–10; O, 15–50; C, 50 to several hundreds; and A, thousands. The symbol B indicates the level of Brown & Sherrard's collections; only single slabs are in their collections, so abundances are unknown.

Systematic palaeontology

Class **Graptolithina** Bronn, 1849

Order **Dendroidea** Nicholson, 1872

Family **Dendrograptidae** Roemer, in Frech, 1897

Dendrograptus J. Hall, 1858

Type species. *Graptolithus hallianus* Prout, 1851; subsequently designated by J. Hall (1862).

Dendrograptus sp.

Fig. 3A

Material. A single specimen AMF 92368, from locality W830, *praecornutus* Biozone, late Ludlow, Black Bog Shale.

Description. The single fragment is a little over 7 mm long, with five branching divisions of typical *Dendrograptus* style. Autothecae are seen in one part and have a spacing of 20 in 10 mm. Dorsoventral stipe width is about 0.40 mm, assuming the lowest stipe is in true profile. Lateral stipe width is 0.15–0.40 mm, declining distally, suggesting that this portion of stipe is towards the extremity of the rhabdosome.

Remarks. *Dendrograptus* is a rare genus in the Silurian of NSW and only one specimen has been found in the Yass district. Rickards & Wright (1997) recorded five unidentifiable fragments from the Barnby Hills Shale; from the Quarry Creek region Rickards *et al.* (1995) recorded sparse, specifically unidentifiable fragments in the Wenlock and others, possibly conspecific with the Wenlock form, at two levels in the early Ludlow. It was suggested in the latter paper that the fragmentary nature of the rhabdosome, which is no less robust than other well-preserved dendroids occurring with them, may indicate a longer and more turbulent preservational history or, perhaps, a more distant, further inshore, provenance.

Dictyonema J. Hall, 1851

Type species. *Gorgonia retiformis* J. Hall, 1843; subsequently designated by Miller (1889).

Dictyonema sp. cf. *D. sherrardae sherrardae* Rickards *et al.*, 1995

Fig. 3B

?1952 *Dictyonema* sp.; Brown & Sherrard, p. 133, pl. VIII, fig. e.
cf. 1995 *Dictyonema sherrardae sherrardae* Rickards *et al.*, p. 20, figs. 11A–C, 12D,E, 13A,B.

Material. A small number of fragmentary specimens including: AMF 92369 from locality W69, Black Bog Shale from Ludlow, pre-*praecornutus* Biozone; and AMF 103037–44 from locality W171, Rosebank Shale, Přídolí, *parultimus* Biozone, ?AMF 44611 (Brown & Sherrard, 1952, pl. VIII, fig. e).

Description. Thecae with pronounced dorsal apertural process occupying fully half of the dorsoventral width of 0.80–0.95 mm and directed ventrally. Autothecal spacing about 20 in 10 mm. Bithecae not detected. Lateral stipe width about 0.30–0.40 mm.

Remarks. This is the first possible record of the *sherrardae* group in the Přídolí, as the two previously known Ludlow occurrences are in the *nilssoni* Biozone (Rickards *et al.*, 1995) and the *inexspectatus-kozlowskii* Biozone (Rickards & Wright, 1997). The Yass material is close to the type subspecies in thecal spacing and dorsoventral stipe width, but we have no data on dissepimental spacing and stipe spacing, and no information on dissepiment type. *Dictyonema s. mumbilensis* Rickards & Wright (1997: 215–216) from the late Ludlow *inexspectatus/kozlowskii* level of the Wellington district (and here reported from Barrandella Shale Member of the Silverdale Formation [Fig. 2] at Yass) is a more slender form with a higher thecal spacing which may represent an offshoot of the main lineage.

Dictyonema elegans Bulman, 1928

Figs. 3C,D

1928 *Dictyonema elegans* sp. Bulman, p. 52, text-fig. 26; pl. 6, figs. 2–3.
1984 *Dictyonema (Dictyonema) elegans* Bulman; Kraft, p. 402; pl. 1, figs. 2–4.
1995 *Dictyonema elegans* Bulman, 1928; Rickards *et al.*, p. 22, figs. 14C,D.
1997 *Dictyonema elegans* Bulman, 1928; Rickards & Wright, p. 214, figs. 5C, 8D.
?1997 *Dictyonema* cf. *elegans* Bulman, 1928; Rickards & Wright, p. 214, fig. 5D.
1997 *Dictyonema ?elegans* Bulman, 1928; Rickards & Wright, p. 214, fig. 6B.

Material. Upper beds of Black Bog Shale, late Ludlow: AMF 92366 from locality W830, *praecornutus* Biozone; AMF 102899 from W831, *cornutus* Biozone. One specimen (AMF 102890) from locality W430, late Přídolí; Elmside Formation, Black Range Road.

Description. Lateral stipe widths up to 0.25–0.30 mm and dorsoventral stipe widths 0.44–0.55 mm, including pronounced ventral processes. No obvious dorsal apertural processes. Interstipe spaces up to 0.40–0.60 mm. Stipe spacing approximately 20 in 10 mm, but the fragments do not allow a good measurement of dissepimental spacing. It is possible that the ventral apertural processes become spinose distally (see Fig. 3C) but these may, in fact, be slender dissepiments. Autothecal spacing about 30 in 10 mm.

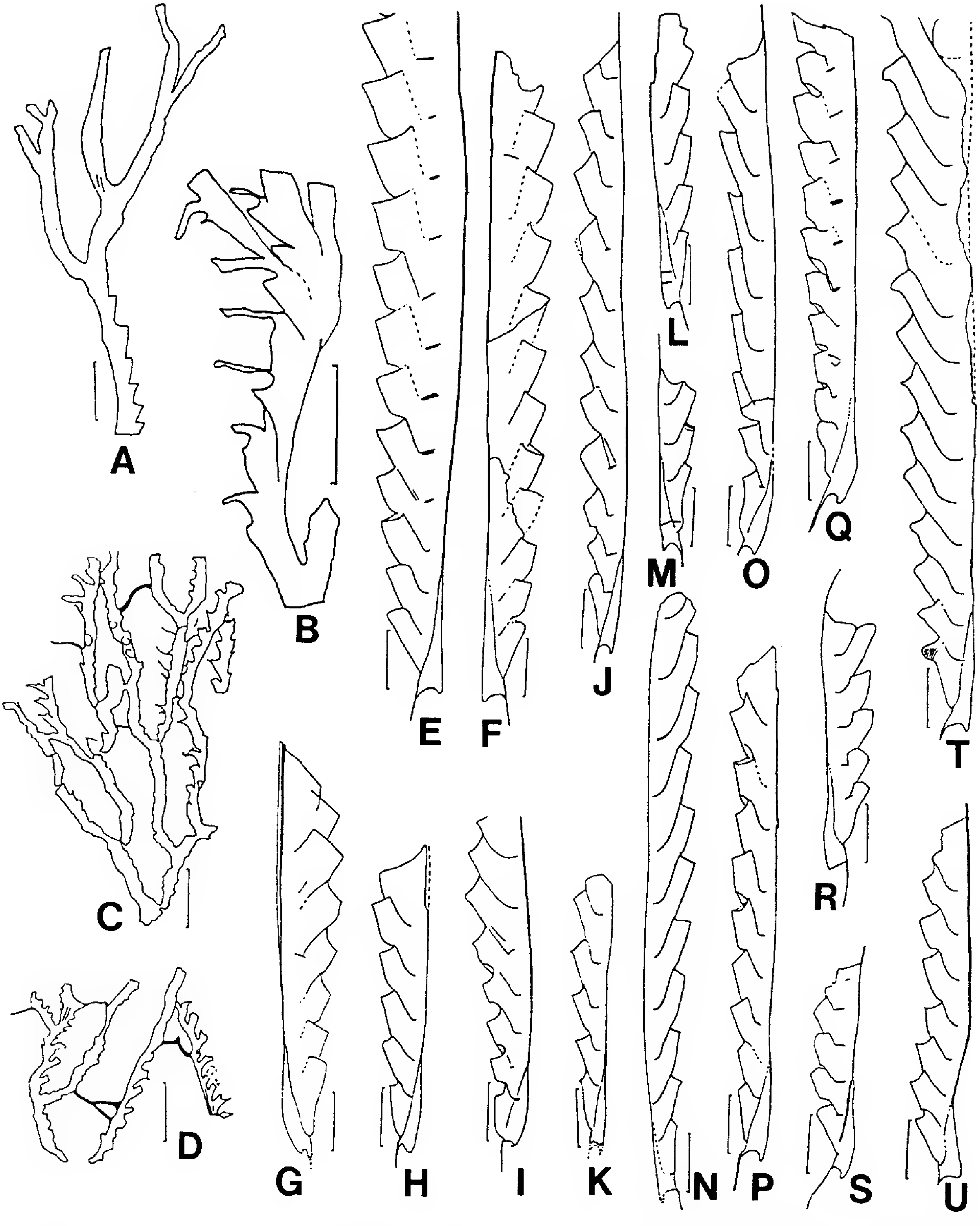


Figure 3. **A**, *Dendrograptus* sp., AMF 92368, W830, Black Bog Shale, *praecornutus* Biozone. **B**, *Dictyonema* sp. cf. *D. sherrardae sherrardae* Rickards *et al*., 1995, AMF 92369, W69, Black Bog Shale, Derringullen Creek. **C,D**, *Dictyonema elegans* Bulman, 1928; respectively AMF 102890, W430, Elmside Formation, *transgrediens* Biozone; and AMF 92366, W830, Black Bog Shale, *praecornutus* Biozone. **E,F**, *Pristiograptus kolednikensis* Přibyl, 1940, respectively AMF 92353–54, probably W171, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek. **G–I**, *Pristiograptus dubius* Suess, 1851, respectively AMF 92359, AMF 92356, AMF 92360, W830, Black Bog Shale, *praecornutus* Biozone. **J–P**, *Pristiograptus shearsbyi* n.sp., respectively AMF 92358, W830, Black Bog Shale, *praecornutus* Biozone; AMF 92385, W833, base of Cowridge Siltstone; AMF 92345, W827, Rosebank Shale, *parultimus* Biozone; AMF 92395, holotype AMF 92392 and AMF 92394, W834, Cowridge Siltstone, *bouceki* Biozone; AMF 92344, W827, Rosebank Shale, *parultimus* Biozone. **Q–S,U**, *Monograptus parultimus* Jaeger, 1975; respectively AMF 102894, W171, Rosebank Shale, *parultimus* Biozone; AMF 92361, W171, Rosebank Shale, *parultimus* Biozone; AMF 92383, W171, Rosebank Shale, *parultimus* Biozone; AMF 92349, W827, Rosebank Shale, *parultimus* Biozone. **T**, *Monograptus transgrediens* Perner, 1899, AMF 92393, W834, Cowridge Siltstone, *bouceki* Biozone. Scale bars 1 mm.

Remarks. Bulman (1928) recorded the species from the late Wenlock and Rickards *et al.* (1995) extended its range into the Ludlow (*nilssoni* Biozone). There seemed to be more variation in the specimens recorded by Rickards & Wright (1997) from the Barnby Hills Shale (*inexspectatus–kozlowskii* Biozone, late Ludlow) and, in addition to *D. elegans*, they recorded *D.* cf. *elegans* and *D. ?elegans*. The last we now feel more confident in placing with the specimens of *D. elegans* of the Barnby Hills Shale: it should be noted that the autothecal spacing of these specimens (at 20 in 10 mm) contrasts with Bulman's originals and with the Quarry Creek specimens (both 25 in 10 mm) as well as with the present material (30 in 10 mm). Thus there is no linear decrease in thecal size from the Wenlock to the late Přídolí, so *D. elegans* presently has little biostratigraphic utility in the Late Silurian. The form described as *D.* cf. *elegans* from the Barnby Hills Shale (Rickards & Wright, 1997) may yet prove to be a new species smaller than, but closely related to, *D. elegans* Bulman.

Order **Graptoloidea** Lapworth, 1875

Family **Monograptidae** Lapworth, 1873

Pristiograptus Jaekel, 1889

Type species. *Pristiograptus frequens* Jaekel, 1889, by original designation.

Pristiograptus kolednikensis Přibyl, 1940

Figs. 3E,F, 4A, 13F

1940	*Monograptus (Pristiograptus) kolednikensis* Přibyl, p. 70, text-figs. 1–8.
1943	*Pristiograptus kolednikensis* Přibyl, 1940; Přibyl, p. 20–21; text-figs. 2I,J; text-figs. 3L,M.

Material. Figured specimens AMF 92353–54 (formerly numbered University of Wollongong F1872), AMF 92365 (formerly University of Wollongong F886) and numerous other specimens (AMF 103090–94, AMF 103102, SM X.28018–22, SM X.28056–57) from localities W171, 827 and 828, *parultimus* Biozone (Přídolí), Rosebank Shale.

Diagnosis. *Pristiograptus* with sicula 2.00–2.20 mm long, apex at level of th 2 aperture; rhabdosome more or less straight; dorsoventral width 0.70–0.90 mm at level of th 1, to 1.12–1.72 mm at th 10 and up to 2.20 mm most distally; thecal spacing 11–12 in 10 mm proximally to 9–10 in 10 mm distally; thecal overlap around ½; thecal inclination 20–30°; thecal aperture of th 1 sometimes slightly rounded, but no other apertural modifications seen. $\Sigma = 1.04–1.10$

Remarks. These specimens are clearly very close to *Pristiograptus fragmentalis* (Bouček, 1936) especially as recently redescribed by Koren′ & Sujarkova (1997) from the late Ludlow of south Tien Shan. They differ only in having a smaller Σ value and in having lower distal dorsoventral width (2.20 mm maximum compared with 2.2–2.8 mm). All previous descriptions of *P. fragmentalis* confirm its high dorsoventral width. Jaeger (*in* Kříž *et al.*, 1986) was of the opinion that the early growth stages of *P. fragmentalis* (and, presumably, very similar forms such as *P. kolednikensis*) were very difficult to distinguish from *P. dubius*. Whilst there is some truth in this, especially when the proximal end shows a slight ventral curvature, it seems to us that not only is the proximal end more commonly straight, but that the angle of thecal inclination of the early thecae is higher in *P. kolednikensis* and *P. fragmentalis* (contrast, for example, Figs. 3E,F and Figs. 3G–I herein; and see Koren′ & Sujarkova, 1997, text-fig. 7). Further comment on the evolution of *P. kolednikensis* is given in the evolution section. The specimen AMF 92365 is shown as Fig. 4A for direct comparison with *M. transgrediens* (Perner, 1899; Figs. 4B–E herein).

This is the first report of this species from Australia.

Pristiograptus dubius (Suess, 1851)

Figs. 3G–I

1850	*Graptolithus colonus* Barr.; Barrande, p. 43, pl. 2, fig. 5.
1851	*Graptolithus dubius* Suess, p. 115, pl. 9, figs. 5a,b.
1943	*Pristiograptus dubius dubius* (Suess, 1851); Přibyl, p. 3, pl. 1, figs. 4–6.
1958	*Pristiograptus dubius* (Suess); Urbanek, p. 83–87, text-fig. 57; pl. 5, figs. 1, 2; text-pl. 7.
1986	*Pristiograptus dubius* (Suess); Koren′, p. 119–122, pl. XXIX–XXX, text-figs. 27–29.

Material. Figured specimens (AMF 92356, 92359, 92360) all from locality W830, *praecornutus* Biozone, Black Bog Shale, late Ludlow; other specimens from the same locality are AMF 103045–52, SM X.28024–28.

Remarks. Although fitting previous descriptions fairly closely, this material exhibits some variation in sicular length from 1.40–1.88 mm. The position of the apex remains the same—midway between the apertures of th 1 and th 2—and in consequence the thecal spacing of the early thecae on those rhabdosomes with a shorter sicula is higher (15 in 10 mm compared with the more usual 12 in 10 mm; see, for example, Figs. 3G,I).

In general, *P. dubius* has been rarely illustrated or described from stratigraphic levels towards the end of its long range (early Wenlock to Přídolí); for example, it was recorded from as high as the *ultimus* Biozone (Přídolí) by Koren′ & Sujarkova (1997) but was neither figured nor described. Bearing in mind that *P. dubius* is one of the longest-ranging lineages (ranging through approximately 18 Ma) it would be useful to document its occurrences carefully. Our material shows a rather more pronounced dorsal sicular tongue (Figs. 3G–I) than do stratigraphically lower forms of *P. dubius*, but we have no way of knowing whether this is a general feature of stratigraphically high forms.

Pristiograptus shearsbyi n.sp.

Figs. 3J–P, 11A,B, 13B,E

Material. HOLOTYPE AMF 92392, locality W834, Cowridge Siltstone, Barambogie Creek, *bouceki* Biozone, Přídolí; specimen in three dimensions. PARATYPES. AMF 92385, locality W835, Rosebank Shale; AMF 92344–45, locality W827, *parultimus* Biozone, Rosebank Shale; AMF 92394–95, locality W834, *bouceki* Biozone, Cowridge Siltstone. Rare at locality W830, Black Bog Shale (AMF 92358), Ludlow. Numerous Přídolí specimens from localities W171, W827, W828, W835, Rosebank Shale; W832, W833, W834 from the Cowridge Siltstone (AMF 102956–60, 103004–12, 103017–18, 103023–25, 103095–101, 103103, SM X.27111–12, SM X.28029–31, SM X.28041–48); and from the Elmside Formation, locality W430 (AMF 102926, AMF 103053).

Etymology. After A.J. Shearsby, photographer and pioneer geologist in Yass.

Diagnosis. Straight, thin *Pristiograptus* rhabdosomes, up to 12 mm long and with a maximum dorsoventral width (flattened) of 0.85 mm; proximal dorsoventral width 0.40–0.55 mm; sicula 1.20–1.65 mm, apex reaching midway between apertures of th 1 and th 2; Σ=1.2–1.4; thecal overlap about ½; thecal inclination 10–30°; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; th 1 very rarely shows a slight rounding of the aperture; sicula with short but pronounced dorsal tongue.

Description. The proximal end is mostly quite straight, but a minority of specimens shows a very gentle ventral curvature (e.g., Figs. 3J,N,O). Occasionally, as in Fig. 3K, the apex of the sicula reaches to the level of the aperture of th 2, and it may be that the difficult-to-see prosicula usually reaches that level. The thecal overlap seems to vary slightly from just under ½ (e.g., Fig. 3J) to almost exactly ½ (Fig. 3N). The rounding seen rarely on th 1 is no more than that commonly seen in *P. dubius*, and all the thecae are essentially pristiograptid in nature. There is a very slight geniculum identifiable in some specimens (Fig. 3P) though not to the extent seen in *Pseudomonoclimacis* Mikhajlova, 1975.

Remarks. This is the first record of a slim pristiograptid from the Yass region in late Ludlow and Přídolí strata; Jaeger (1967) referred to pristiograptids of the *dubius* group from the Rosebank Shale, but not from the Cowridge Siltstone where we have found them commonly with *M. bouceki* and *M. transgrediens* on Barambogie Creek. Similarly the slender *Crinitograptus* and *Neocucullograptus* from localities W171, W827 and W828, which we describe below, have not been previously reported from these localities, although they also occur with *P. shearsbyi* n.sp. Koren′ & Sujarkova (1997) recorded *P. dubius* from as high as the *ultimus* Biozone and *P.* ex gr. *dubius* from a little higher (*tumultuosus* Biozone: they are not described or figured herein).

Other slender pristiograptids of the *dubius* group occur from the late Llandovery to the middle Ludlow. Usually they are of short duration, repeatedly arising from the stem lineage of *P. dubius*, and are difficult to distinguish one from another in view of the few available biocharacters. *Pristiograptus shearsbyi* n.sp. differs from earlier slender pristiograptids, however, in having a pronounced dorsal tongue to the sicular aperture, a feature which affects many graptoloid lineages in the late Ludlow and Přídolí. The more robust *P. dubius* (Figs. 3G–I) is similarly affected at this stratigraphic level. In lacking thickening at the base of the interthecal septum, this species is distinct from *Pseudomonoclimacis*.

Monograptus Geinitz, 1852

Type species. *Lomatoceras priodon* Bronn, 1835; subsequently designated by Bassler (1915).

Remarks. In this paper we follow the taxonomy of Koren′ & Sujarkova (1997, p. 66–67) in using a broadly-conceived *Monograptus*, arguing that recognition of genera such as *Istrograptus* Tsegelnjuk, 1988, *Scalograptus* Tsegelnjuk, 1976 and *Neocolonograptus* Urbanek, 1997 is premature: a better understanding of the evolutionary lineages is necessary before these taxa can be accepted. Although some monograptids may have arisen from a pristiograptid stock, there has been no serious suggestion that they should be referred to a taxon such as "*Pristiograptus*".

Brown & Sherrard (1952) illustrated taxa attributed to *Monograptus bohemicus* (Barrande, 1850) from portion 15, parish of Hume; this specific identification has, hitherto, remained unchallenged. To date, only Jaeger (1967) has commented again on these monograptids; he believed there were two subspecies of *Monograptus bohemicus* present through what is essentially the upper section of the Black Bog Shale covered by our localities W830 to W831. Here we distinguish three species-level taxa of curved, *bohemicus*-type graptoloids, which we identify as *Bohemograptus tenuis, B. paracornutus* n.sp. and *B. praecornutus* Urbanek, 1970. No *B. b. bohemicus sensu stricto* has been confirmed from Yass as yet, although an ample thickness of the Black Bog Shale exists below our locality W830. Further, the "*M. bohemicus*" illustrated by Brown & Sherrard (1952, see locality map fig. 1) is from just below our localities W832 and W833 on "Tulla Park", despite the fact that they did have Rainbow Hill material collected by Gordon Packham (pers. comm., GHP). The material illustrated by Brown & Sherrard (1952, fig. 2d; pl. VIII, fig. d) as *M. bohemicus* is actually *M. b. tenuis* (Fig. 12B). Our re-identifications of the names they assigned to the illustrated graptolites are given in Table 1.

Monograptus parultimus Jaeger, 1975

Figs. 3Q–S,U

1968 *Monograptus* sp., cf. *Monograptus ultimus* Perner; Packham, p. 219–220; pl. 11, figs. 1–3, 5, 6.
1975 *Monograptus parultimus* Jaeger, p. 119–125, text-fig. 44; pl. 2, figs. 4, 8.
1986 *Monograptus parultimus* Jaeger, 1975; Jaeger *in* Kříž *et al.*, p. 318–321, text-figs. 29–34; pl. 1, figs. 1, 2, 5, 8, 9; pl. 2, figs. 3–6, 23, 24; pl. 4, fig. 12.
1988 *Ludensograptus parultimus* (Jaeger, 1975); Tsegelnjuk, p. 82, fig. 5.
1990 *Pseudomonoclimacis parultimus* (Jaeger, 1975); Lenz, p. 1081, figs. J–L.
1992 *Monograptus parultimus* Jaeger, 1975; Rickards & Banks, p. 10–11, fig. 1B; pl. 1B.
1997 *Monograptus parultimus* Jaeger; Koren′ & Sujarkova, p. 78–79, text-figs. 12A–Y; pl. 4, figs. 5–12; pl. 5, figs. 1–7.

[Further references were given by Jaeger (*in* Kříž *et al.*, 1986) and Rickards & Banks (1992)]

Material. Fairly common at Přídolí localities W171, W827 and W828 (AMF 92349, AMF 92361 [formerly numbered University of Wollongong F 520], AMF 92383–84, AMF 102894, AMF 103076, SM X.28023, SM X.28049), *parultimus* Biozone, Rosebank Shale; rare at Přídolí locality W835, possibly in Přídolí localities W832–3 (AMF 103019–22), post-*parultimus* Biozone, all low in Cowridge Siltstone.

Diagnosis. *Monograptus* with rhabdosomes usually less than 10 mm long and with a maximum dorsoventral width of about 1.30 mm at that length; proximal end and sicula often with slight ventral curvature; sicula with dorsal tongue and virgella often directed at 45° to the rhabdosomal axis; thecal apertures undulating, with slight elevations, especially th 1–th 3, thereafter declining somewhat, and often with thickened rims; thecal spacing proximally 11–13 in 10 mm; distal thecal spacing 9–11 in 10 mm; thecal overlap <½; slight geniculum; base of interthecal septum often thickened; Σ=1.1–1.5; sicula 1.70–1.90 mm; dorsoventral width at th 1, 0.60–0.80 mm; dorsoventral width at th 10, 1.00–1.40 mm.

Remarks. Our material is very close to the type material from Kosov Quarry (Jaeger *in* Kříž *et al.*, 1986), but is a little different in dimensions from the specimens described recently from south Tien Shan (Koren′ & Sujarkova, 1997) which are slightly wider and have a higher Σ value. The Yass specimens are also close to the Tasmanian specimens described by Rickards & Banks (1992), differing only in having slightly more of a geniculum as, indeed, does the type material; this is almost certainly a reflection of preservational differences. Sherwin (1979, p. 161) stated that the taxon identified by Packham (1968) as *M.* cf. *ultimus* was believed to be *M. tomczyki*.

Monograptus transgrediens Perner, 1899 *sensu lato*

Figs. 3T, 4B–E, 11C, 13A

1899 *Monograptus transgrediens* Perner, p. 13, pl. 17, fig. 24.
1940 *M. (Pristiograptus) transgrediens* Perner; Přibyl, p. 68–69.
1943 *Pristiograptus transgrediens* Perner; Přibyl, p. 30–31; pl. 2, fig. 7; pl. 3, fig. 7.
1964 *M. transgrediens* (Perner); Teller, p. 52, pl. 2, fig. 3; pl. 3, figs. 1–4; pl. 7, figs. 8–12.
1982 *Monograptus transgrediens* Perner 1899; Jenkins, p. 171, fig. 3M, N(?).
?1982 *Monograptus transgrediens* cf. *praecipuus* Přibyl, 1940; Jenkins, p. 171, figs. 3G,H.
1984 *Monograptus transgrediens transgrediens* Perner, 1899; Porebska, p. 141–144, figs. 13, 1–9.
1986 *Monograptus transgrediens* Perner; Koren′, p. 115–116, text-figs. 1–6, 25; pl. 27, figs. 1–6; pl. 28, figs. 1–5.
1986 *Monograptus transgrediens* Perner, 1899; Jaeger *in* Kříž *et al.*, p. 326–328, text-figs. 41a–c; pl. 1, figs. 15, 17, 18; pl. 2, figs. 12, 16, 17, 19, 22, 25.
1990 "*Pristiograptus*" *transgrediens* (Perner); Lenz, p. 1081, figs. P–R.
1997 *Monograptus transgrediens* Perner, 1899; Koren′ & Sujarkova, p. 81–83, text-figs. 15A–P; pl. 6, figs. 3–9.
1997 *Istrograptus transgrediens transgrediens* (Perner, 1899); Teller, p. 76–77; pl. 2, figs. 1–11.

Material. Common at locality W834 (AMF 92387, AMF 92389, AMF 92390, AMF 92391, AMF 92393), low in Cowridge Siltstone, Barambogie Creek, *bouceki* Biozone, Přídolí; and a few specimens from W430 (AMF 102927a, AMF 102939–47, AMF 102966–68, SM X.27094–100), Elmside Formation, Black Range Road, *transgrediens* Biozone, Přídolí.

Diagnosis. *Monograptus* with proximal end usually with slight ventral curvature, and rounding of the thecal apertures (raised lappets) visible sometimes even on th 7, though more commonly on th 1 to th 5; sicula with slight ventral curvature, dorsal tongue, a length of 1.60–1.90 mm, Σ=1.3–1.5, and an apex which reaches to the level of between the apertures of th 1, and th 2 (though with the prosicula not often visible); proximal thecal spacing 10–13 in 10 mm, distally about 10 in 10 mm; dorsoventral width at th 1 0.70–0.80 (in three dimensions) and distally 1.30–1.50 mm (three dimensional specimens). Rhabdosomes in the Elmside Formation reaching a length of 30 mm and a dorsoventral width of 1.80 mm.

Remarks. The type material was redescribed by Jaeger (*in* Kříž *et al.*, 1986) and our material is close to that except in being shorter and hence less robust; Jaeger (*in* Kříž *et al.*, 1986) recorded a maximum length of 100 mm and a maximum width of 3 mm. Although Koren′ & Sujarkova

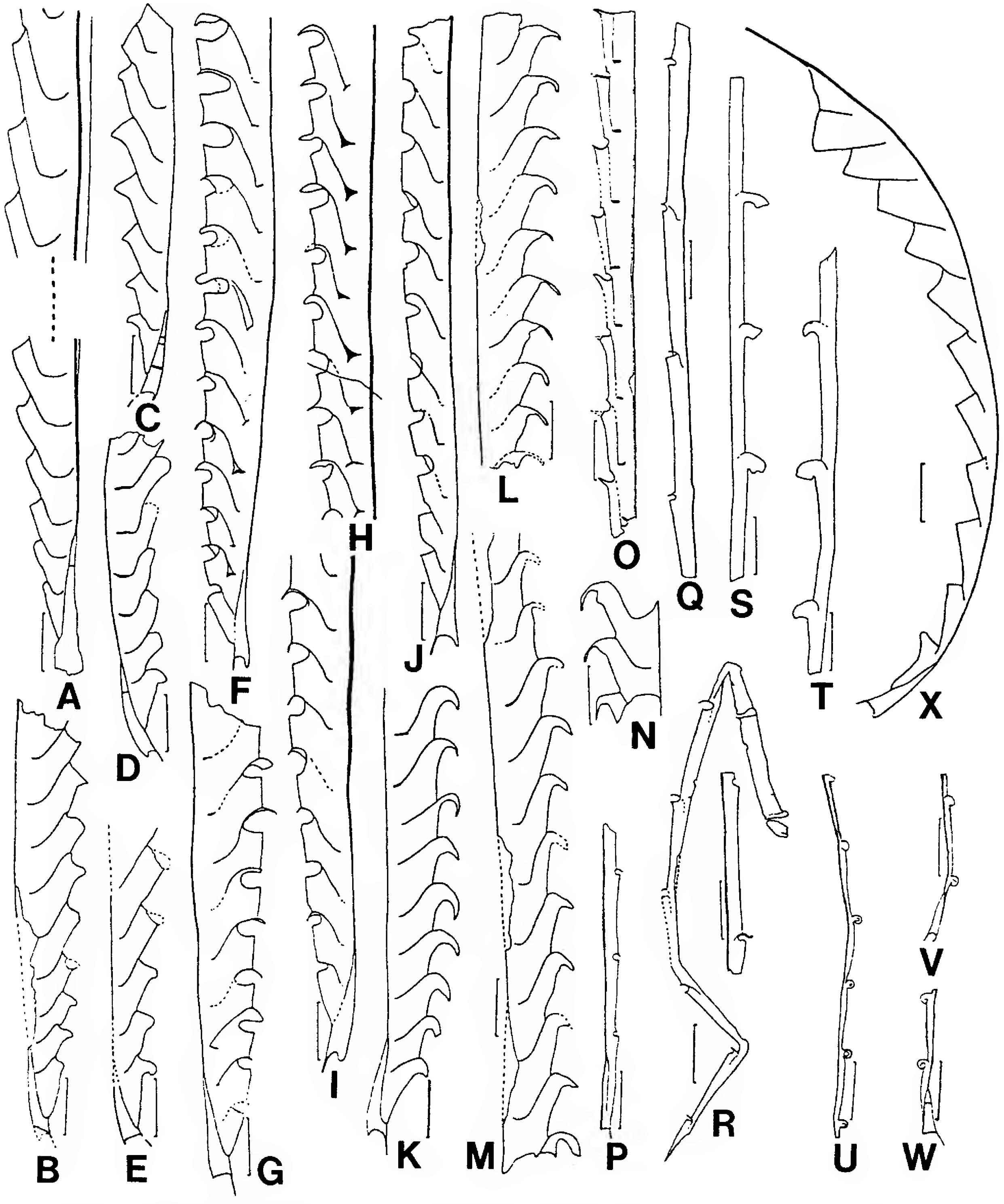


Figure 4. **A**, *Pristiograptus kolednikensis* Přibyl, 1940, AMF 92365, W171, Rosebank Shale, *parultimus* Biozone, for direct comparison with *M. transgrediens* (B–E). **B–E**, *Monograptus transgrediens* Perner, 1899, respectively AMF 92389, AMF 92391, AMF 92387, AMF 92390, W834, Cowridge Siltstone, *bouceki* Biozone. **F–I**, *Monograptus pridoliensis* Přibyl, 1981; respectively AMF 92352, AMF 92347, AMF 92351, AMF 92350, W827, Rosebank Shale, *parultimus* Biozone. **J**, *?Monograptus pridoliensis* Přibyl, 1981, AMF 92355, W171, Rosebank Shale, *parultimus* Biozone. **K–N**, *Monograptus bouceki* Přibyl, 1940, respectively, after Jaeger (1967, pl. 14, fig. A), AMF 92388, 92386, 92386b, W834, Cowridge Siltstone, *bouceki* Biozone. **O**, *Monograptus* sp. indet, AMF 102889, W834, Cowridge Siltstone, *bouceki* Biozone. **P–R**, *Crinitograptus operculatus* (Münch, 1938) respectively AMF 102891, AMF 102892, W171, Rosebank Shale, *parultimus* Biozone; and AMF 92342, W828, Rosebank Shale, *parultimus* Biozone. **S,T**, *Neocucullograptus? mitchelli* n.sp., holotype AMF 102895, W171, Rosebank Shale, *parultimus* Biozone. **U–W**, *Neocucullograptus? yassensis* n.sp., respectively AMF 92346, AMF 92344, holotype AMF 92343, W828, Rosebank Shale, *parultimus* Biozone. **X**, *Bohemograptus bohemicus tenuis* (Bouček, 1936), AMF 92339, W830, Black Bog Shale, *praecornutus* Biozone. Scale bars 1 mm.

(1997) commented on Jaeger's (*in* Kříž *et al.*, 1986) redescription of Perner's types, they did not refer to Jaeger's topotype material in their synonymy: the dimensions and form of their southern Tien Shan specimens are, however, very close to the Bohemian types. The Σ value is less in the types than either the southern Tien Shan material or the Yass material, both of which agree closely in this feature.

Monograptus transgrediens is a typical and long-ranging Přídolí species. Teller (1997) suggested that the number of beak-like thecae in "*Istrograptus*" increased gradually through the Přídolí, with "*Istrograptus*" *t. transgrediens* being typical of the highest levels with several beak-like thecae. However, our *bouceki* Biozone material has one to seven beak-like thecae, and the *transgrediens* Biozone Elmside Formation forms have far fewer, suggesting that more study of the described subspecies on a wider geographical basis is required before firm subspecific assignment can be achieved. Although Jenkins (1982) did not identify his figures 3M and 3N, we presume they represent his *M. transgrediens.* We are uncertain about the form he ascribed to *M. t.* cf. *praecipuus* (Jenkins' figs. 3G,H) and include it doubtfully in our synonymy of *M. transgrediens.* Jaeger (1967) noted that there were two forms present of *M. transgrediens* but we cannot confirm this from our material which may have a range of sizes from smaller earlier growth stages to "normal" late growth stages.

Monograptus pridoliensis Přibyl, 1981

Figs. 4F–I,?J, 13D

1940 *Monograptus (Pomatograptus) similis* Přibyl, p. 72, text-figs. 1, 3; pl. 1, fig. 5.
1981 *Monograptus pridoliensis* nom. nov.; Přibyl, p. 371–372, text-figs. 1, 3–6; pl. 1, fig. 1; pl. 2, fig. 6.
1986 *Monograptus pridoliensis* Přibyl, 1981; Jaeger *in* Kříž *et al.*, p. 328–330, text-fig. 42; pl. 3, figs. 1, 12; pl. 4, figs. 2, 3, 8, 9, 11.
1990 *Monograptus* cf. *pridoliensis* Přibyl; Rickards & Garratt, p. 43–44, figs. 4a–f.

Material. Numerous specimens from localities W171, W827, W828 (AMF 92347–48, AMF 92350–51, AMF 92352, ?AMF 92355 (formerly University of Wollongong F 1872), AMF 103077–89, SM X.28052–55), *parultimus* Biozone, Rosebank Shale, Přídolí.

Diagnosis. *Monograptus* with more or less straight rhabdosome but with dorsal margin showing slight ventral curvature over the first few thecae; sicula effectively straightens the rhabdosome outline, even giving a slight dorsal flexure (Fig. 4F) in some specimens; sicula 1.50–2.0 mm long; Σ=1.2–1.5; sicular apex almost to level of second thecal aperture; dorsal sicular tongue; slight ventral curvature of sicula common; thecae with pronounced hoods which lessen a little distally; thecal overlap about ½ proximally, base of interthecal septum being above the level of the preceding aperture, increasing distally to more than ½; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; dorsoventral width proximally 0.65–0.80 mm; at th 10 is 1.40–1.70 mm and most distally is 2.00 mm.

Remarks. Our material so closely resembles that described by Rickards & Garratt (1990) as *M.* cf. *pridoliensis*, from the Přídolí part of the Humevale Formation of Victoria, that we include the latter in synonymy with *M. pridoliensis*. At most, the only difference is the very slightly more slender proximal end of the Yass material (0.65–0.80 mm compared with 0.70–0.90 mm at the level of th 1). From the type material redescribed by Jaeger (*in* Kříž *et al.*, 1986) our material differs only in having the hood slightly less developed.

In Bohemia *M. pridoliensis* is recorded only from the eponymous biozone, above that of *lochkovensis*, whereas our material is unquestionably from the earlier *parultimus* Biozone. Koren′ (1983), however, recorded *M. similis* from the *formosus* Biozone of Kazakhstan, so our record from Yass is not stratigraphically out of place in a global sense; this Kazakhstan material has been redescribed as *M. bessobaensis* Koren′, 1986. The differences between *M. pridoliensis* and other similar species such as *M. prognatus* Koren′, 1983 were discussed by Koren′ (1983) and Rickards & Garratt (1990) and will not be repeated here, but the evolutionary possibilities of the form are outlined in the section on evolution.

Monograptus bouceki Přibyl, 1940

Figs. 4K–N, 12A, 13C

1937 *Monograptus flemingii* (Salter); Sherrard & Keble, p. 313, pl. XV, figs. 4, 5, text-figs. 20–22.
1940 *Monograptus (Pomatograptus) bouceki* Přibyl, p. 71, text-fig. 1, pl. 1, figs. 7, 8.
1952 *Monograptus salweyi* (Hopkinson); Brown & Sherrard, p. 132, pl. VIII, figs. a,b; text-figs. 2b,c.
1967 *Monograptus bouceki* Přibyl; Jaeger (not described), pl. 14A.
1986 *Monograptus bouceki* Přibyl, 1940; Jaeger *in* Kříž *et al.*, p. 331–332, pl. 3, figs. 3, 7–11, 13, 15.
1986 *Monograptus bouceki* Přibyl, 1940; Koren′, p. 97–99, pl. XX, figs. 2–4; text-fig. 15.
1997 *Monograptus bouceki* Přibyl, 1940; Koren′ & Sujarkova, p. 71–73, text-fig. 9B–D,I–L; pl. 1, fig. 8; pl. 2, figs. 1–9.
1997 *Monograptus bouceki* Přibyl, 1940; Koren′ (*in* Nikitin & Bandaletov), p. 97–99, pl. 20, figs. 2–4; text-fig. 15.

[Fuller synonymies are given in Jaeger (*in* Kříž *et al.*, 1986) and in Koren′ & Sujarkova (1997)]

Material. Numerous specimens from locality W834, *bouceki* Biozone, Cowridge Siltstone, Barambogie Creek (AMF 92386, AMF 92388), Přídolí. We have restudied AMF 44608, the specimen illustrated as *Monograptus salweyi* (Hopkinson) by Brown & Sherrard (1952, pl. VIII, fig. b); it is re-illustrated here (Fig. 12A), but does not appear to be a specimen illustrated by Sherrard & Keble (1937).

Diagnosis. *Monograptus* with more or less straight rhabdosome, but often with a slight dorsal flexure proximally caused largely by the position of the sicula (Fig. 4K); sicula 1.65 mm long (seen, but possibly incomplete); Σ=1.3; apex of sicula below level of hood of th 2; sicula with ventral curvature; dorsal tongue present; proximal dorsoventral width 0.90–1.10 mm; distal dorsoventral width up to 1.50–2.00 mm; proximal thecal spacing 11–12 in 10 mm; distal thecal spacing 9–10 in 10 mm; thecae claw-like in profile with strong development of dorsal thecal wall only; thecal overlap always ½ or less; thecal inclination 35–40°.

Remarks. The Yass material seems to differ from the types only in being a little more slender throughout; indeed Jaeger's (1967) original figure (pl. 14, fig. A: reproduced herein as Fig. 4K) was also of a slightly slender form. Material described by Koren′ & Sujarkova (1997) is a little more robust, but is otherwise identical. *Monograptus bouceki* appears in the eponymous biozone and ranges higher, just into the *transgrediens* Biozone at the top of the Přídolí (Jaeger, *in* Kříž *et al*., 1986).

Monograptus formosus
Bouček, 1931b

Monograptus formosus jenkinsi n.subsp.

Figs. 11M,N, 13J

1982 *Monograptus* cf. *formosus* Bouček, 1931b; Jenkins, p. 171, fig. 3E.

Material. HOLOTYPE, ANU 35910, only specimen as part and counterpart, from the Elmside Formation, Black Range Road, NW of Yass (see Jenkins, 1982, p. 167); *transgrediens* Biozone, late Přídolí.

Etymology. For Dr C.J. Jenkins, who first described this specimen.

Diagnosis. *Monograptus formosus* with slender rhabdosome no more than 0.88 mm in dorsoventral width; thecal spacing of 8–9 in 10 mm; thecal hook occupying about one half the rhabdosomal width; dorsal thecal wall strongly retroverted, pointing almost dorsally at its distal extremity; free ventral wall inclined at about 15°; thecal overlap very low, less than one sixth.

Remarks. The new subspecies differs from the type subspecies not only in being half as wide but also in having the prothecal wall inclined at a lower angle throughout the rhabdosome (15° compared with 20–30°), in having less thecal overlap (compare Figs. 11M,N with 11K,L) and in having a lower thecal height (up to 1.30–1.40 mm in the type subspecies). The thecal spacing of *M. f. jenkinsi* n.subsp. is identical with that of the type subspecies as described by Jaeger (1967) and Packham (1968) from the Rosebank Shale (Figs. 11J–L herein). The nature of the thecal hooks (not lappets) appears to be the same in both taxa except that they are wider and higher in the type subspecies. *Monograptus uncatus* Koren′ & Sujarkova, 1997 has similar width and comparable thecal spacing.

This is the only occurrence of this species at Yass, other than the stratigraphically lower occurrence in the *formosus* Biozone (Jaeger, 1967; Packham, 1968) which is, as stated above, late Ludlow to earliest Přídolí.

Monograptus hornyi
Jaeger (*in* Kříž *et al*., 1986)

Figs. 11D–G, 13G

1982 *Monograptus* cf. *angustidens* Přibyl, 1940; Jenkins, p. 169–170, figs. 3F,I–L,O–Q.

1986 *Monograptus hornyi* Jaeger; *in* Kříž *et al*., p. 330–331, pl. 3, figs. 2, 6: pl. 4, figs. 16–17.

Material. Numerous well preserved specimens, many in three dimensions, from the Elmside Formation, W430, Black Range Road, *transgrediens* Biozone, Přídolí. Figured specimens AMF 102920–21, AMF 102923–24; other specimens are SM X.27113–17 and AMF 102922, AMF 102948–55, AMF 103002–03.

Diagnosis. *Monograptus* with rhabdosome up to 5.5 cm long with a maximum, distal, dorsoventral width of 2.20 mm; proximal end with characteristic gentle dorsal flexure affecting up to 7 thecae, occasionally almost straight; sicula emphasizes dorsal curvature of rhabdosome, but itself is often with strong ventral curvature, so that the extremely robust virgella points proximoventrally; sicula 1.30–1.65 mm long (mean 1.58), apex reaching above the level of the hood of th 1, sometimes to the level of the hood of th 2; thecae strongly hooked and claw-like throughout; overlapping at most ½ half distally; spaced at 12–15 in 10 mm proximally and 9–10 in 10 mm distally; thecal hook is a dorsal hood with little or no growth of the ventral apertural margin; some lateral expansion of the hood is likely; Σ=1.2 mm.

Remarks. Jenkins (1982) placed specimens from this locality in the *M. angustidens*–*M. uniformis* group, but the mesial and distal thecal overlap of ½ in *M. hornyi* preclude reference to *M. uniformis* as thecal overlap is much greater in the Lower Devonian species group. *Monograptus bouceki* is the most closely-related species, but *M. hornyi* has a shorter sicula: 1.5–1.8 mm in the type locality, 1.4–1.6 mm in the Elmside locality, compared with 1.80–2.22 mm in *M. bouceki* (Jaeger *in* Kříž *et al*., 1986; Koren′ & Sujarkova, 1997). The Σ values are also lower in *M. hornyi* (1.2 at Elmside; 1.2–1.3, usually, in the type material, compared with 1.2–1.6 in *M. bouceki*). The characteristic proximal curvature of the Elmside specimens contrasts with straighter rhabdosomes of *M. bouceki* from locality W834 (Fig. 2) but specimens of *M. bouceki* described by Koren′ &

Sujarkova (1997) from South Tien Shan do show similar curvature to *M. hornyi* from the Elmside Formation. The known stratigraphical ranges of *M. bouceki* and *M. hornyi* are, respectively, *bouceki* to *transgrediens* biozones and *lochkovensis* to *perneri* biozones; further documentation of these rarely recorded species may establish their morphological and evolutionary limits. *Monograptus hornyi* differs from *M. pridoliensis*, which we also describe from the Yass district in that the latter has less retroverted hoods so that the ventral thecal wall is commonly visible and the hooks appear more beak-like than hooked, especially distally. *Monograptus prognatus* Koren′, 1983 has much greater thecal overlap than *M. hornyi*, already apparent by th 15. The Elmside specimens reach a greater dorsoventral width than in Jaeger's (*in* Kříž *et al.*, 1986) type material, but the latter are shorter rhabdosomes: at comparable lengths the dorsoventral width is the same. The robust virgella seen in the Elmside specimens is a feature of old age and thus is not seen in the type material which only rarely reaches 30 mm long (usually less than 20 mm).

Monograptus perneri
Bouček, 1931a

Monograptus perneri elmsidensis n.subsp.

Figs. 11H,I, 13H,I

Material. HOLOTYPE AMF 102922 (part and counterpart) and PARATYPE AMF 103001 both from locality W430, Elmside Formation, Black Range Road, *transgrediens* Biozone, late Přídolí.

Etymology. This subspecies takes its name from the nearby property Elmside (Fig. 1).

Diagnosis. *Monograptus perneri* with unusually narrow rhabdosome, no more than 0.75 mm dorsoventral width, and a slightly straighter rhabdosome than *M. p. perneri* Bouček, 1931a or *M. p. kasachstanensis* Mikhajlova, 1975 but still with dorsal curvature; thecal spacing 10–11 in 10 mm; thecal overlap about a half; thecal hook occupies a third of overall rhabdosomal width; thecal hook retroverted, seemingly pointing proximally; sicula 1.80 mm long, with ventral curvature, apex reaching midway between the apertures of th 1 and th 2, short dorsal process, small virgella; Σ=1.44 mm.

Remarks. *Monograptus perneri elmsidensis* n.subsp. is straighter and conspicuously narrower than *M. p. perneri* and *M. p. kasachstanensis* Mikhajlova, 1975 whilst retaining the overall rhabdosomal aspect and thecal style. The thecal spacing is lower than the other subspecies and the Σ value greater; because of the thin rhabdosome, the interthecal septa are almost parallel to the axis. We have found only the two specimens amongst several hundred graptolites collected at the locality, so it must be considered a rare component of the fauna.

Monograptus sp. indet.

Fig. 4 O

Material. One specimen lacking a proximal end, in full profile and three dimensions, AMF 102889, from locality W834, *bouceki* Biozone, Přídolí. Cowridge Siltstone, Barambogie Creek.

Remarks. This striking specimen has low-angled thecae with an overlap around ½ thecal apertures with thickened lips, and a similarly thickened base to the interthecal septum. It seems to resemble none of the described species at this level, nor any in the late Ludlow. There is a slight geniculum, but apparently no hood, and the ventral apertural lip may be slightly denticulate. It may represent the distal thecae of a biform species. *Monograptus balticus* Teller, 1966 has similar dimensions in its distal thecae but our form has less overlap and lacks thecal hoods; *Monograptus microdon aksajensis* Koren′, 1993 is closer on thecal overlap but this form has thecal hoods on its distal thecae.

Crinitograptus Rickards, 1995

Type species. *Monograptus crinitus* Wood, 1900, by original designation.

Crinitograptus operculatus
(Münch, 1938)

Figs. 4P–R

1938	*Barrandeograptus operculatus* Münch, p. 53–68, text-figs. 2a–c; pl. 8, figs. 1, 2, 5, 6, 11; pl. 9, figs. 4, 5.
non 1952	*Monograptus crinitus* Wood; Brown & Sherrard, p. 132–133, text-fig. 2a.
?1955	*Barrandeograptus operculatus* (Münch); Kühne, p. 397–399, figs. 18A–F.
1995	*Crinitograptus operculatus* (Münch); Rickards, fig. 3.2.

Material. Fairly common at localities W171, W827, W828 (AMF 92342, AMF 102891–93, AMF 103104–06, SM X.28032–39), *parultimus* Biozone, Přídolí. Rosebank Shale.

Diagnosis. *Crinitograptus* of typically slender dimensions and fragile appearance, maximum dorsoventral width 0.40 mm, proximally 0.25–0.28 mm; sicula 1.20 mm long; apex well below level of aperture of th 1; Σ=1.7; sicular aperture without noticeable tongue; thecal apertures small, semicircular excavations with a genicular hood and slightly undulating lateral and ventral margin; thecal overlap obscure, but may be small; proximal thecal spacing 7 in 10 mm falling to 4 in 10 mm most distally; thecae uniform; thecal inclination almost 0°; nema conspicuously more sclerotised than remainder of colony; virgella tiny.

Remarks. Rickards (1995) placed this species in synonymy with the type species *C. crinitus*, but they are here considered distinct. In the latter the thecal spacing is closer distally (5 in 10 mm proximally, 7 in 10 mm distally) whereas the reverse is true in *C. operculatus*, and the thecal spacing is lower. *Crinitograptus crinitus* is typically a low Ludlow species and *C. operculatus* a Přídolí form in the Yass area. This is the first report of the genus from Australia.

Brown & Sherrard (1952, p. 132, text-fig. 2e) described a specimen (AMF 44615) from one (not specified) of their "*M. bohemicus*" localities as *Monograptus crinitus* Wood. This specimen is less slender and has quite different cited thecal spacings to those seen in our specimens; we conclude that the material represents proximal portions of *Linograptus p. posthumus* which occurs commonly at the "*M. bohemicus*" level.

Neocucullograptus Urbanek, 1970

Type species. *Neocucullograptus kozlowskii* Urbanek, 1970, by original designation.

Remarks. Two forms are described tentatively (perhaps temporarily) under this genus as no other genus appears to be an appropriate place for them. They show neocucullograptine features including the proximal end and possibly typical thecal hooks, but are distinct in their tiny dimensions; in the rock they are inconspicuous in the extreme and might easily be overlooked in the field.

Neocucullograptus? yassensis n.sp.

Figs. 4U–W, 13L,M

Material. HOLOTYPE AMF 92343, locality W828. PARATYPES AMF 92344 (locality W828) and AMF 92346 (locality W827). Both localities *parultimus* Biozone, Přídolí, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek.

Etymology. After the Yass district of New South Wales.

Diagnosis. Minuscule neocucullograptid rhabdosome with a dorsoventral width ranging from 0.20–0.24 mm, more or less straight; sicula 0.75 mm extending about half way along th 1; possible dorsal process; Σ=1.10–1.25; thecae with "hooks" of unknown structure; thecal spacing 7–9 in 10 mm close to the proximal end, 9–10 in 10 mm more distally; free ventral wall almost parallel to rhabdosomal axis with small amount of late prothecal expansion; thecal overlap small, but not clear; thecal "hook" occupying about half the rhabdosomal width; dorsoventral width immediately prior to "hook" is 0.10–0.12 mm.

Remarks. Although the proximal end looks like described neocucullograptines it is much smaller and narrower, with a sicula only half the length of that of *N. inexspectatus* Urbanek, 1970 and only one third that of *N. kozlowskii* Urbanek, 1970. We can equate *N.? yassensis* with no other species group at present; its proper generic attribution must remain in doubt until more material is available.

Neocucullograptus? mitchelli n.sp.

Figs. 4S,T

Material. HOLOTYPE, AMF 102895 (part and counterpart), locality W171, *parultimus* Biozone, Přídolí, Rosebank Shale, near crossing of Hume Highway and Derringullen Creek.

Etymology. After John Mitchell, pioneer geologist in the Yass district.

Diagnosis. Minuscule neocucullograptine rhabdosome with dorsoventral width of 0.50–0.70 mm including "hook"; excluding hooks the parallel-sided metathecal part has a width of only 0.20–0.30 mm; proximal end not known, but thecal spacing constant at 4.5 in 10 mm; thecal overlap obscure, probably small; thecal inclination 0°; thecal hook occupies about half the rhabdosome width; thecal "hook" obscure, apparently facing ventrally.

Remarks. This species is quite unlike any previously-described form in the Ludlow or Přídolí. The thecal "hooks" are quite unlike the apertural hoods in *Crinitograptus*, and are different from the possibly enrolled "hooks" in *N.? yassensis* n.sp. Both *N.? yassensis* n.sp. and *N.? mitchelli* n.sp. **may** have the neocucullograptine style of apertural processes but this is not certain.

Bohemograptus Přibyl, 1967

Type species. *Graptolithus bohemicus* Barrande, 1850, by original designation.

Bohemograptus praecornutus Urbanek, 1970

Figs. 5C–L, 13K

1970	*Bohemograptus praecornutus* Urbanek, p. 301–310, text-fig. 16; pl. 20C; pls 23, 24.
1976	*Bohemograptus arcuatus* Tsegelnjuk, p. 128, pl. 40, figs. 6–9.
?1976	*Bohemograptus urbaneki* Tsegelnjuk, p. 129, pl. 40, figs. 10–12.
1990	*Bohemograptus praecornutus* Urbanek; Lenz, figs. 3Q,R.
1995	*Bohemograptus praecornutus* Urbanek, 1970: Štorch, p. 71–72, text-figs. 3C,I; text-figs. 4A,E,G; pl. 1, fig. 4; pl. 3, figs. 4, 7.
1997	*Bohemograptus praecornutus* Urbanek; Urbanek & Teller, pl. 4, fig. 9.

Material. Numerous specimens from locality W830, *praecornutus* Biozone, late Ludlow, Black Bog Shale, Rainbow Hill, AMF 92303, AMF 92331–34, AMF 92336–38, AMF 102898, AMF 103026–36, AMF 103171–72; SM X.28050–55.

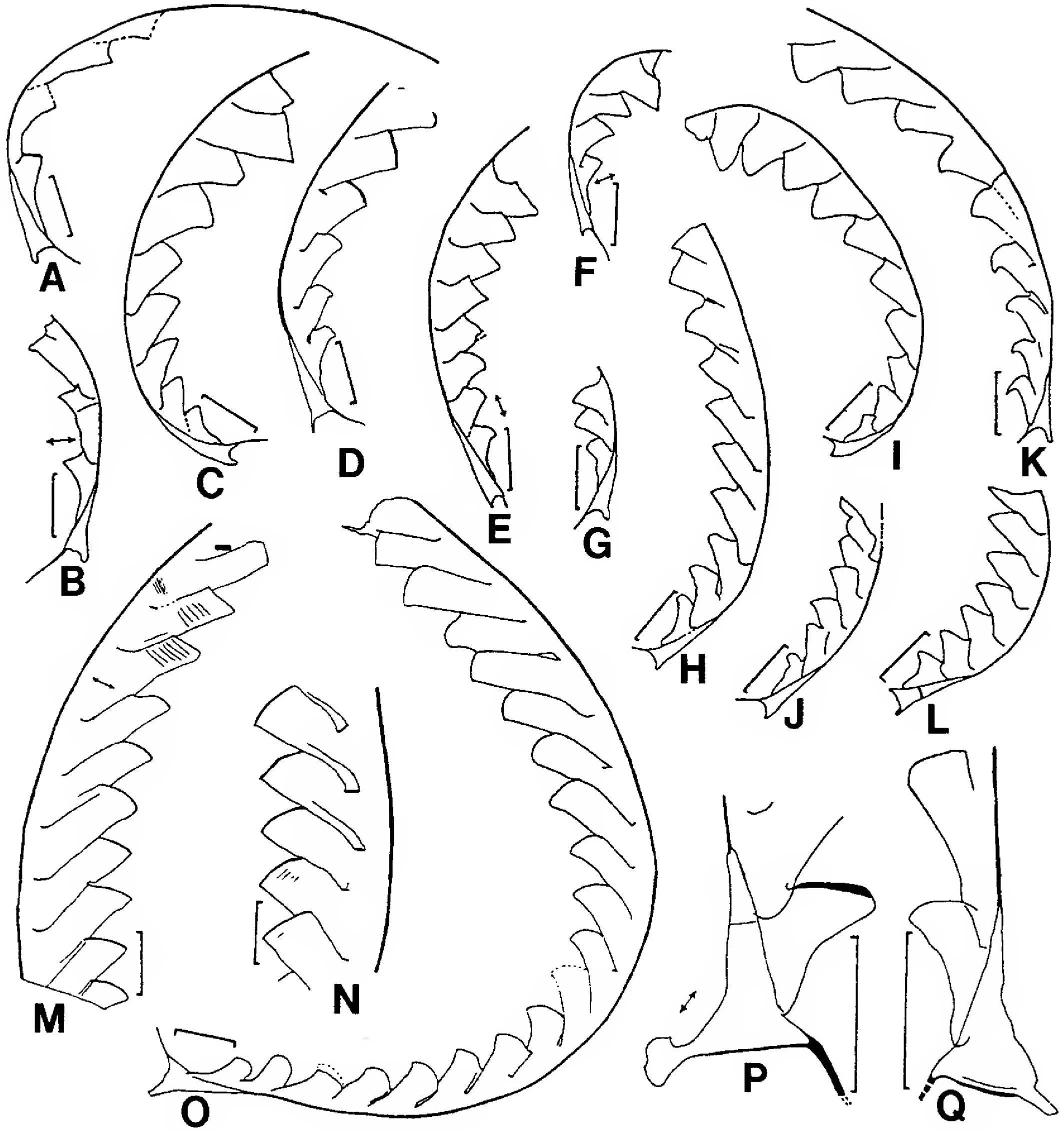


Figure 5. **A,B**, *Bohemograptus bohemicus tenuis* (Bouček, 1936), respectively AMF 92341, AMF 92340, both W830, Black Bog Shale, *praecornutus* Biozone. **C–L**, *Bohemograptus praecornutus* Urbanek, 1970, respectively AMF 92334, AMF 102898, AMF 92338, AMF 92335, AMF 92332, AMF 92331, AMF 92337, AMF 92333, AMF 92303, AMF 92336, all W830, Black Bog Shale, *praecornutus* Biozone. **M–Q**, *Bohemograptus paracornutus* n.sp., respectively AMF 92323, AMF 92311, AMF 92324, AMF 92322, AMF 92302, all W831, top of Black Bog Shale, *cornutus* Biozone. D, K and L show the maximum apertural widening seen in *B. praecornutus*. Scale bars 1 mm.

Diagnosis. *Bohemograptus* with tight ventral curvature and relatively robust rhabdosome with a distal dorsoventral width of up to 1.40 mm at 10 mm from the sicula; dorsoventral width at th 1, 0.45–0.70 mm, at th 10, 0.80–1.30 mm; sicula 1.10–1.50 mm; apex midway between apertures of th 1 and th 2; sicula straight or ventrally curved, with pronounced dorsal tongue directed dorsally; proximal thecal spacing 12–18 in 10 mm; distal thecal spacing as low as 10 in 10 mm; most thecal apertures rounded or with undulating margins; proximal thecae often slightly isolated in profile; thecal overlap about ½ throughout; thecal inclination 40–50°.

Remarks. The sicular length is closer to Urbanek's (1970) type material than to Štorch's (1995) recent description of Bohemian specimens, but our material partly overlaps with both. Otherwise the material is very close to previous descriptions on all counts. One specimen (Fig. 5K) may have the veliger morph features recorded by Urbanek (1970) but is not well preserved; it is the only one possibly showing such features. The differences from *B. paracornutus* n.sp. are discussed under the following description. This is the first report of the species from Australia. Dr T. Koren′ (pers. comm.) has informed us that *B. urbaneki* Tsegelnjuk, 1976 differs from *N. praecornutus*

Urbanek in having a larger sicula with a higher position of the apex, smaller dorsoventral width and weaker gradient of rhabdosomal widening.

Bohemograptus paracornutus n.sp.

Figs. 5M–Q, 6A–N, 7, 9A,B, 10A–E

Material. HOLOTYPE AMF 92317. Figured PARATYPES AMF 92301–02, AMF 92305–08, AMF 92311, AMF 92319–30, AMF 92363–64; other specimens among the available thousands include: AMF 102969–103000, AMF 103054–75, SM X.27178–242. All from from *cornutus* Biozone, late Ludlow, topmost Black Bog Shale, Rainbow Hill, locality W831.

Etymology. This name draws attention to the similar precursor *B. praecornutus*.

Diagnosis. *Bohemograptus* of relatively robust proportions, with strong ventral curvature so that rhabdosomes are approximately semicircular with the thecae on the inside (Fig. 6A,B). Sicula with spectacular apertural expansion so that the sicula is trumpet-shaped; length 1.36–1.52 mm; apex reaching mid way between the th 1 and th 2 apertures; apertural width 0.90–1.50 mm; prosicula about 0.50 mm; metasicular expansion begins sharply when the sicula is about half grown; dorsal sicular lip with pronounced, often winged, process, directed dorsally, proximally or (rarely) ventrally; rest of sicular aperture (the lateral margins) convexly curved, and strongly thickened; virgella robust, spike-like, directed proximoventrally, up to 1 mm long. Dorsoventral width at th 1, 0.60–1.00 mm; at th 5, 0.90–1.30 mm; and most distally up to 2.00 mm; proximal thecal spacing 12–16 in 10 mm, distally 10–12 in 10 mm; th 1 with markedly concave free ventral wall; subsequent thecae have more or less straight free ventral wall inclined at 40–60°, sometimes slightly concave below the apertures; thecal apertures rounded or undulating, thickened, with lateral elevations with arched fuselli; thecal overlap < ½ proximally and > ½ distally; Σ=1.00–1.28.

Remarks. *Bohemograptus paracornutus* n.sp. is clearly very close to *B. praecornutus*, which it resembles in rhabdosome size, shape, thecal type and thecal spacing, and in the position of the apex of the sicula. Both can be contrasted in this last aspect with *B. b. tenuis*, in which the sicular apex is **below** the level of the aperture of th 1 and the whole proximal end is slim rather than robust. *Bohemograptus paracornutus* n.sp. differs from *B. praecornutus* in its spectacularly expanded sicula. All the specimens we have, numbering in the thousands, show this feature; and of all the specimens of *B. praecornutus* we have examined from locality W830 none has an expanded sicular aperture, Figs. 5K,L being the only specimens showing a very slight expansion. The evolutionary relationship of *B. paracornutus* n.sp. to *B. praecornutus* is discussed in the earlier section on evolution of the Yass fauna. *Bohemograptus paracornutus* n.sp. differs from *B. paratenuis* n.sp. (proposed below) in that the latter has the *B. b. tenuis* style of proximal end, that is rather slim and with the apex of the sicula below the level of the aperture of th 1 and thecae inclined at a much lower angle (20°; see Fig. 4X, Figs. 5A,B).

The NSW geological literature is replete with references to *Monograptus bohemicus* or *Bohemograptus bohemicus* from Yass, mostly simply following Brown & Sherrard (1952) and not being based (in many cases) on actual specimens; it is impossible to speculate on the veracity of these records. However, material illustrated by Brown & Sherrard (1952) is here assigned to *B. b. tenuis*.

Bohemograptus paratenuis n.sp.

1970 *Bohemograptus bohemicus* aff. *tenuis* Bouček, 1936); Urbanek, p. 299, pl. 19.

Material. HOLOTYPE: we nominate the un-numbered specimen in Urbanek (1970, Plate XIX, figure B) as holotype. PARATYPES: five specimens figured by Urbanek (1970, plate XIX, figs. A, C, D, E and F). All material figured by Urbanek in Plate XIX is from the erratic boulder S. 234, Mochty, Poland. The repository is the Palaeozoological Laboratory, Warsaw University. The type material was examined by Rickards in 1986.

Etymology. To indicate relationship to *Bohemograptus b. tenuis* (Bouček, 1936), as discussed in the biostratigraphy and evolution section.

Diagnosis. *Bohemograptus* with trumpet-shaped sicula, the apex of which is located below the level of the aperture of th 1, or no higher than it: angle of free ventral wall of th 1, 10–20°, gently concave; origin of th 1 well above the sicular aperture (0.30–0.35 mm); several metasicular thickened bands, one on the pro/metasicular boundary; pseudo-microfusellar additions to thecal apertures; sicular aperture 0.60–0.70 mm with pronounced and winged dorsal process, directed dorsally or proximally; Σ=1.46–1.56.

Remarks. As suggested by Urbanek, this species is close to *Bohemograptus b. tenuis* (Figs. 5A,B, 4X) but shows the same morphological relationship to that species as *B. paracornutus* n.sp. does to *B. praecornutus*, namely the development of a trumpet-shaped sicular aperture. *Bohemograptus paratenuis* n.sp. differs from *B. paracornutus* n.sp. and *B. praecornutus* in having the origin of th 1 much farther away from the sicular aperture, in the much lower angle of inclination of the free ventral wall of th 1, in the greater Σ value, and in the more proximal position of th apex of the sicula. The trumpet shaped sicula is also narrower than in *B. paracornutus* n.sp.

Egregiograptus Rickards & Wright, 1997

Type species. *Monograptus egregius* Urbanek, 1970; by original designation.

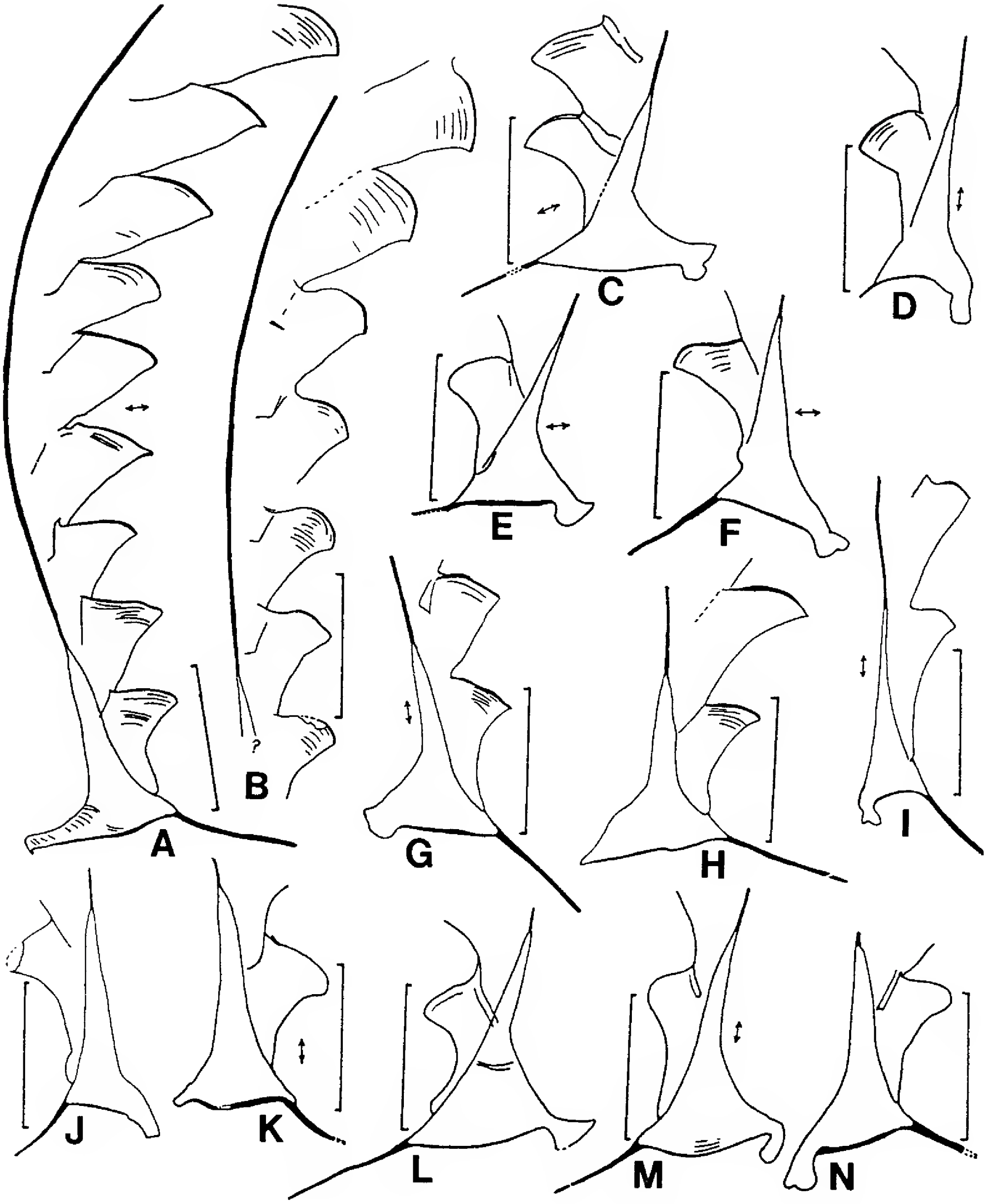


Figure 6. A–N, *Bohemograptus paracornutus* n.sp., respectively AMF 92306, AMF 92305, AMF 92328, AMF 92308, AMF 92326, AMF 92307, AMF 92320, AMF 92319, AMF 92321, AMF 92301, AMF 92325, AMF 92330, AMF 92327, AMF 92329, all W831, top of Black Bog Shale, *cornutus* Biozone. Scale bars 1 mm; tectonic stretching indicated by arrows, where appropriate.

Egregiograptus sp. indet.

Fig. 12C

Material. AMF 44614.

Remarks. Brown & Sherrard (1952, pl. VIII, fig. g) illustrated graptolites on a small slab as *Monograptus roemeri* (Barrande). Most of the specimens are here identified as *Bohemograptus bohemicus tenuis*, but one fragmentary specimen is here assigned to *Egregiograptus*. Sherwin (1979, p. 161) referred this material to the Barrandian species *M. butovicensis*; this species is the type species of *Polonograptus* Tsegelnjuk, 1976, which is a genus that must yet be used with caution (Urbanek & Teller, 1997; Rickards & Wright, 1999) as the type species is poorly known.

Linograptus Frech, 1897

Type species. *Dicranograptus posthumus* Richter, 1875; by original designation.

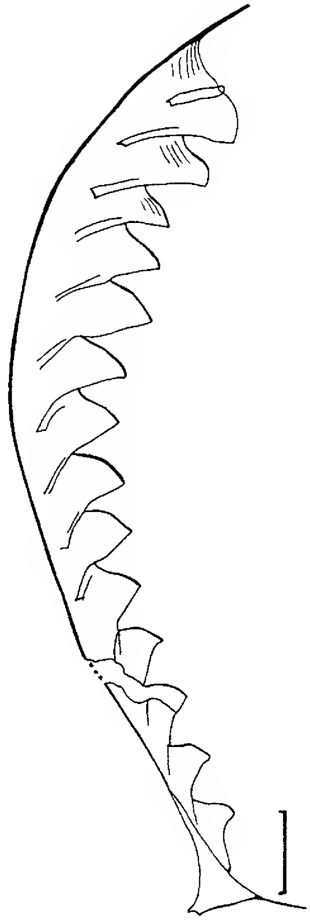


Figure 7. *Bohemograptus paracornutus* n.sp., holotype AMF 92317, W831, top of Black Bog Shale, *cornutus* Biozone.

Remarks. The type subspecies, *Linograptus p. posthumus* (Fig. 8A–C), ranges at Yass from high in the Black Bog Shale in the *cornutus* Biozone to the Přídolí lower part of the Elmside Formation, where it occurs locally in high abundance (Fig. 2). *Linograptus posthumus introversus*, described by us from the late Ludlow Barnby Hills Shale near Wellington, occurs at Yass at collection level 3 (Fig. 8D), a few metres higher than the lowest occurrence of the type subspecies as reported by Brown & Sherrard (1952) as *Monograptus crinitus* (see above under *Crinitograptus*).

Graptolite biostratigraphy

Figure 2 shows the ranges of the Yass graptolites plotted against the established lithostratigraphy, chronostratigraphy and biostratigraphy. Earlier records, such as those of Jaeger (1967), Packham (1968) and Jenkins (1982) are included but not records of out-of-date names in the form of previous identifications, which are listed in Table 1. Most of the species we have listed in Fig. 2 are new records and include several new species. Twenty-seven taxa are recognised, compared with the sparse faunas previously recognised for the Yass area. It is important to recognise that we have not collected through numerous stratigraphic sections, as this is precluded by the exposures: rather, we have collected from mostly previously recognised localities which are well-controlled stratigraphically, as shown on Fig. 1. Placement within a Biozone is not possible in the Yass district occurrences, particularly in view of the discontinuous nature of the graptolite record.

The stratigraphically lowest reported graptolites are all dendroids from the Barrandella Shale Member of the Silverdale Formation in the Yass district and include: those mentioned by Jaeger (1967) from low in the unit; Shearsby's (1912) earlier report; and *Dictyonema* sp. cited by Cramsie *et al.* (1978) from low in the member at Hattons Corner. In a late stage of the preparation of this manuscript, *Dictyonema sherrardae mumbilensis* Rickards & Wright, 1997 was collected from the member in the Yass River upstream from Hattons Corner; we have not seen any dendroid material noted by other authors (Shearsby, 1912; Jaeger, 1967; Cramsie *et al.*, 1978).

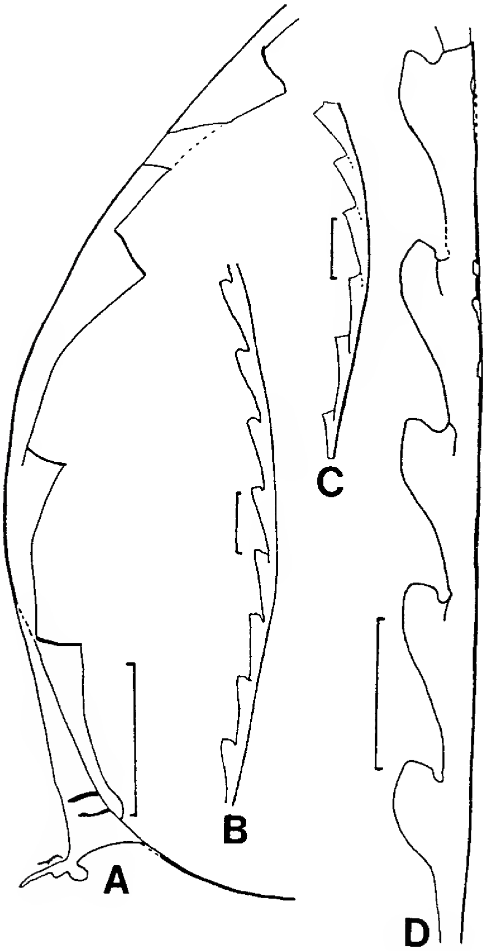


Figure 8. **A–C**, *Linograptus posthumus posthumus* Richter, 1875, respectively AMF 92314, W830, Black Bog Shale, *praecornutus* Biozone; AMF 102897, W171, Rosebank Shale, *parultimus* Biozone; AMF 92367, W830, Black Bog Shale, *praecornutus* Biozone. **D**, *Linograptus posthumus introversus* Rickards & Wright, 1997, AMF 92304, W831, top of Black Bog Shale, *cornutus* Biozone. Scale bars 1 mm.

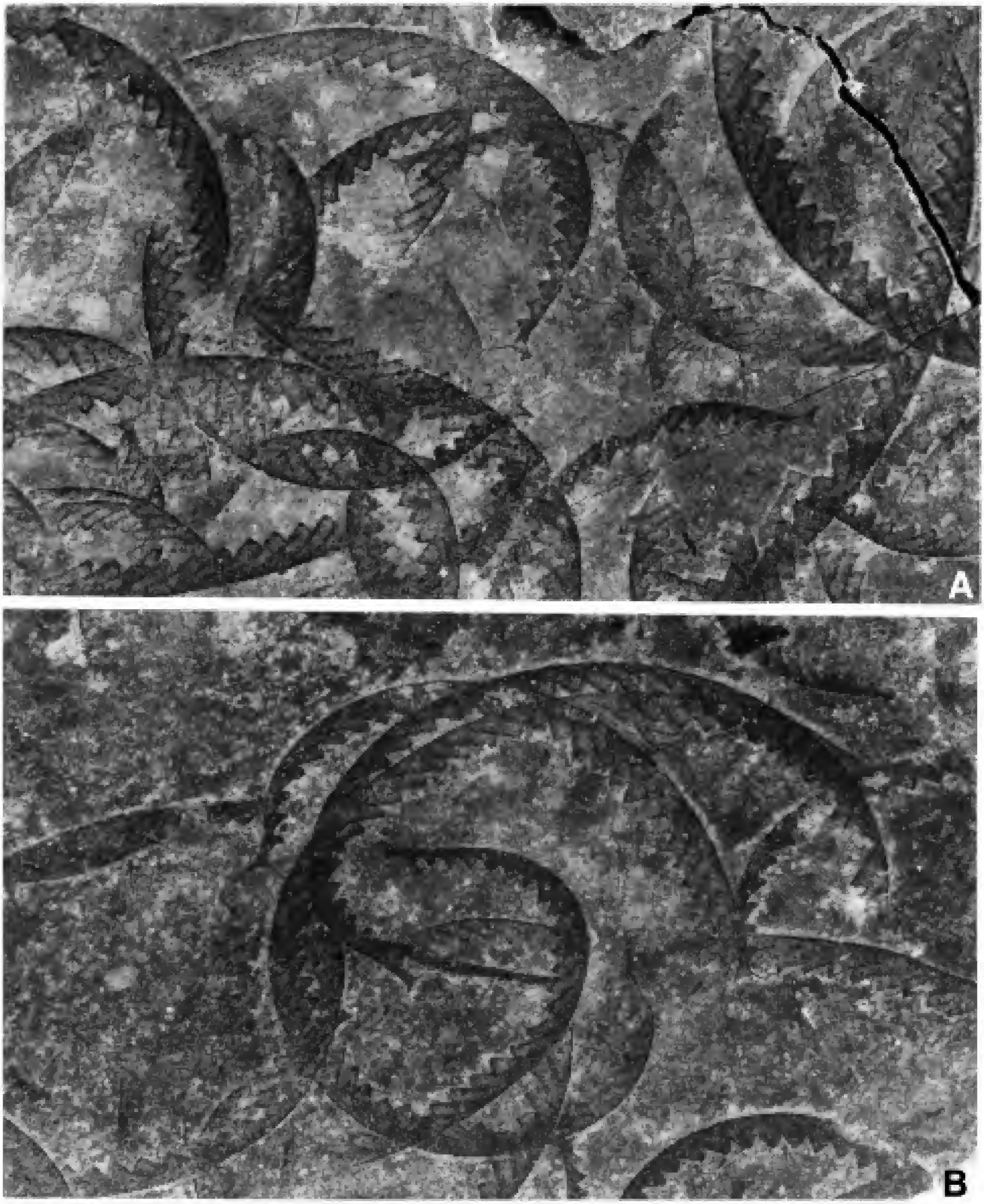


Figure 9. **A,B**, *Bohemograptus paracornutus* n.sp., W831, top of Black Bog Shale, *cornutus* Biozone: A—AMF 92364, B—AMF 92363. ×5.

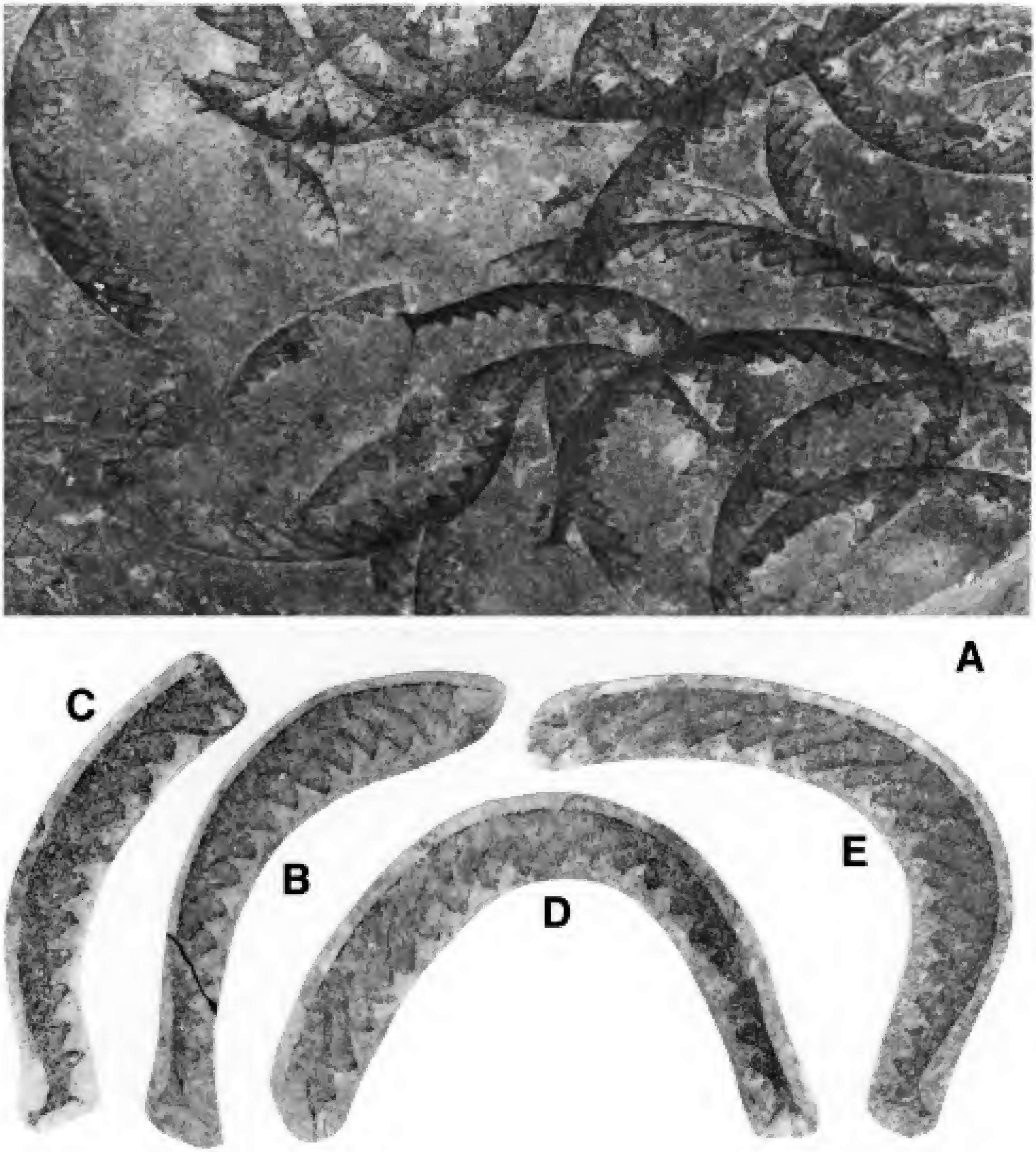


Figure 10. **A–E**, *Bohemograptus paracornutus* n.sp., top of Black Bog Shale, late Ludlow, Rainbow Hill, W831, *cornutus* Biozone, late Ludlow. A, slab AMF 92364, ×5; B, holotype AMF 92317, ×8; C–E, paratypes AMF 92322–24, all ×8.

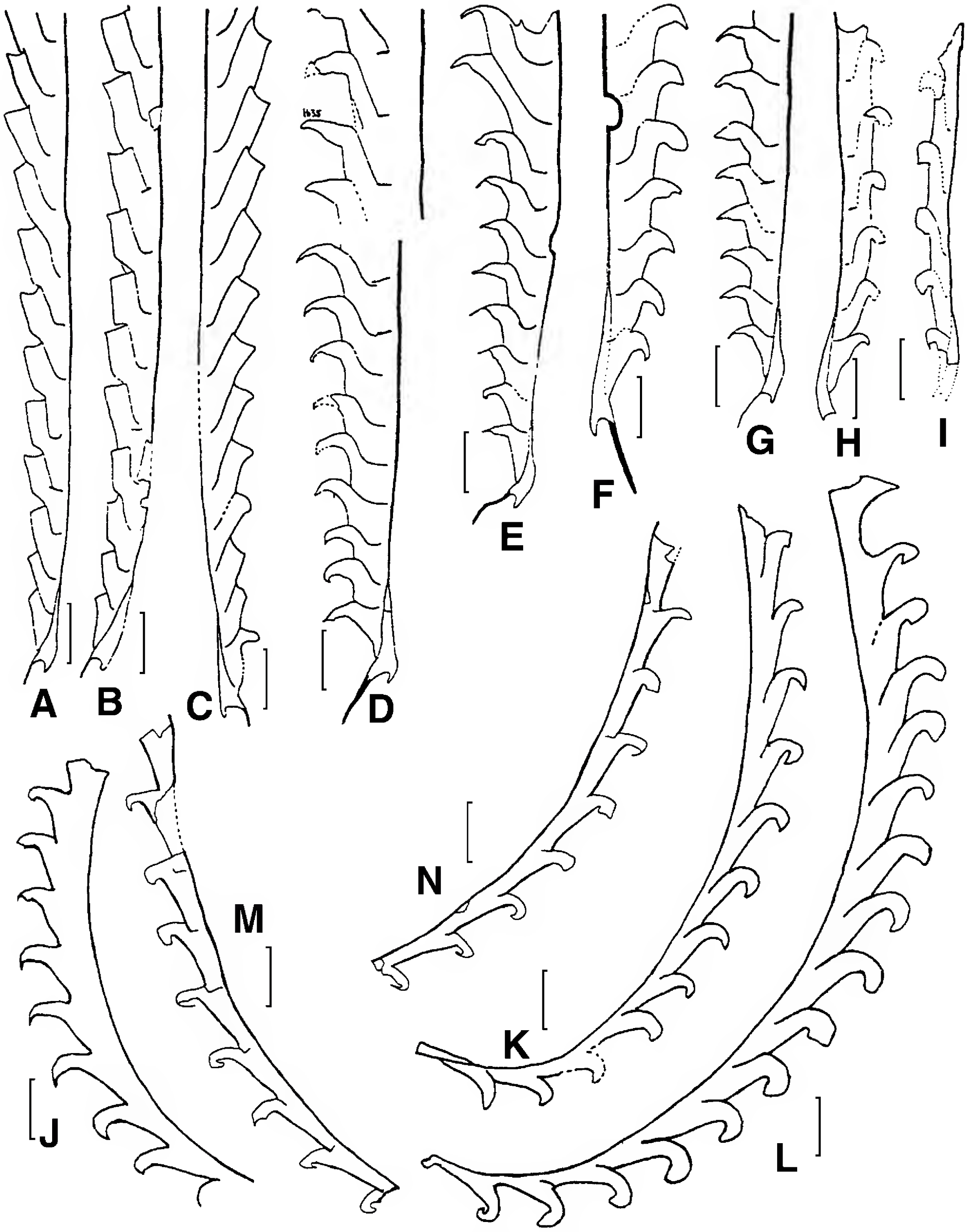


Figure 11. A–N, Graptolites from the Elmside Formation, *transgrediens* Biozone, Black Range Road, NW of Yass, W430. A,B, *Pristiograptus shearsbyi* n.sp., respectively AMF 102925, AMF 102926. C, *Monograptus transgrediens* Perner, 1899, AMF 102927a. D–G, *Monograptus hornyi* Jaeger (*in* Kříž *et al.*, 1986), respectively AMF 102920, AMF 102923, AMF 102924, AMF 102921. H,I, *Monograptus perneri elmsidensis* n.subsp., respectively holotype AMF 102922, and paratype AMF 103001. J–L, *Monograptus formosus formosus* Bouček, 1931b, respectively redrawn from Jaeger (1967, pl. 14b,c) and Packham (1968, pl. 11.4: AMF 71942, formerly SUP 23260), Derringullen Creek, Rosebank Shale, level 4 of Fig. 2. M,N, *Monograptus formosus jenkinsi* n.subsp., holotype ANU 35910, part and counterpart. Scale bars 1 mm.

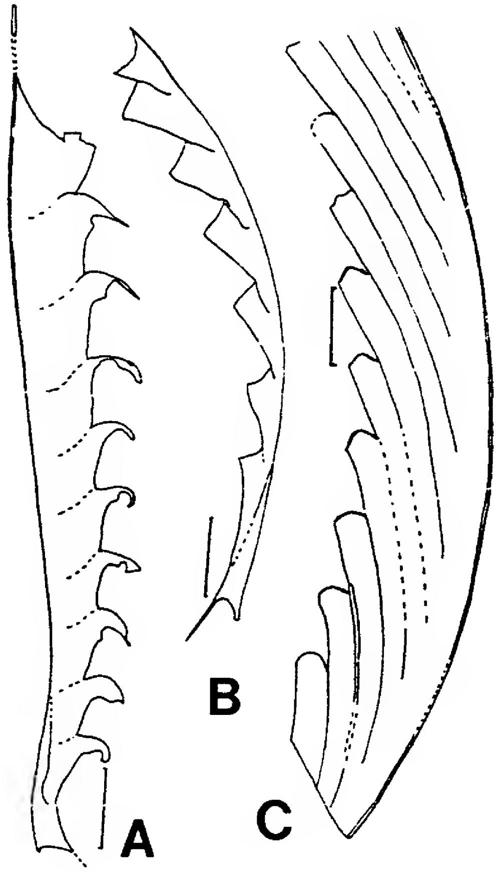


Figure 12. Selected Brown & Sherrard (1952) graptolites. **A**, *Monograptus bouceki* Přibyl, 1940, AMF 44608, Přídolí, Cowridge Siltstone, illustrated as *Monograptus salweyi* (Hopkinson, 1880) by Brown & Sherrard (1952, fig. 2b, pl. VIII, fig. b). **B**, *Bohemograptus b. tenuis* (Bouček, 1936), on same slab as Fig. 12C herein, AMF 44614, Ludlow, from Black Bog Shale (on same slab as *Egregiograptus* sp., but not figured by Brown & Sherrard, 1952). **C**, *Egregiograptus* sp., AMF 44614, Ludlow, Black Bog Shale; illustrated by Brown & Sherrard (1952, fig. 2f, pl. VIII, fig. g) as *Monograptus roemeri* (Barrande, 1850). Scale bars 1 mm.

COLLECTION LEVEL 1. The single specimen we record from our level 1, in the Yarwood Siltstone Member of the Black Bog Shale, is substantially higher stratigraphically than the records mentioned above. The occurrence of *Dictyonema* sp. cf. *D. sherrardae* Rickards *et al*., 1995 at Yass is noteworthy, as it ranges in our collections from level 1 (Ludlow) up to level 4 (Přídolí). The species has previously been recorded as high as the *kozlowskii* Biozone in the Ludlow (Rickards & Wright, 1997) but not in the Přídolí.

COLLECTION LEVEL 2. Locality W830 at Rainbow Hill is where the upper part of the Black Bog Shale has yielded a rich assemblage, including the first record of *Bohemograptus praecornutus* Urbanek, 1970 in Australia.

In his preliminary comments on Yass graptolites from approximately this level, Jaeger (1967) distinguished "two subspecies of *M. bohemicus*", one a "lower subspecies ... the classical *M. bohemicus* subsp. A, which has rather simple thecae", and the other "with elaborated proximal thecae and sicula, is confined to the four metres immediately below the *Dalmanites* Bed", at our collection level 3. Jaeger's second form is almost certainly that described in this paper as *Bohemograptus paracornutus* n.sp. It is related to the *B. cornutus* lineages of Urbanek (1970) rather than to the *B. bohemicus* lineages *sensu stricto*. The exact nature of Jaeger's *B. b.* subsp. A is less certain; it may be the form which we describe below as *B. praecornutus* but, if so, its thecae are very similar to those of *B. paracornutus*. Alternatively, it may be that Jaeger identified *B. b. tenuis*, in which case his collection lacked *B. praecornutus*.

The stratigraphic significance is that *B. praecornutus* ranges, according to Urbanek (1970), through the eponymous biozone up into the succeeding *B. cornutus* biozone where it is less common. So locality W830, which yields *B. praecornutus* in abundance some 10–15 m below the *Dalmanites* Bed, is probably referable to the late Ludlow *praecornutus* Biozone, which is in agreement with our other data. Professor T. Koren′ (pers. comm.) has informed us that *praecornutus* ranges through the upper *scanicus*, *leintwardinensis* and *podoliensis* Biozones in central Asia.

COLLECTION LEVEL 3. Locality W831 at Rainbow Hill is in the top 2–3 m of the Black Bog Shale, and has yielded a small graptolite fauna (accompanied by sparse ceratiocarid debris, and occasional bivalves including *Cardiola* [Sherrard, 1960], ostracodes and small brachiopods) but nothing very distinctive except for the exceedingly abundant, complete, mature specimens of *B. paracornutus* n.sp. As a new species without any other known occurrences, it has no obvious stratigraphic value. However, we argue below, in the section dealing with evolution, that it derives directly from *B. praecornutus*; it is very likely, therefore, that it occurs at the *cornutus* Biozone level. *Bohemograptus cornutus* Urbanek, 1970 is, according to Urbanek (1970), itself a direct derivative of *B. praecornutus*. We have not found *B. cornutus* in the Yass sequence, nor has it been recorded previously from Australia; it is possible that *B. paracornutus* n.sp. and *B. cornutus* occupy different biogeographic provinces. It seems likely, then, that level three is approximately referable to the *cornutus* Biozone in global correlative terms. Presumably there is also a case, which we have not adopted here, for establishing a local *paracornutus* Biozone.

Figure 13 [continued from p. 209]. ... **E**, *Pristiograptus shearsbyi* n.sp., holotype AMF 92392, CowridgeSiltstone, Barambogie Creek, W834, Přídolí, ×10. **F**, *Pristiograptus kolednikensis* Přibyl, AMF 92353, W827, Rosebank Shale, Barambogie Creek, *parultimus* Biozone, Přídolí, ×10. **G**, *Monograptus hornyi* Jaeger, AMF 102923, Cowridge Siltsone, Barambogie Creek, W834, Přídolí, ×10. **H,I**, *Monograptus perneri elmsidensis* n.subsp., Elmside Formation, W430, Black Range Road, *transgrediens* Biozone, late Přídolí, both ×10; H, holotype AMF 102922; I, paratype AMF 103001. **J**, *Monograptus formosus jenkinsi* n.subsp., holotype ANU 35910, Elmside Formation, late Přídolí, Black Range Road, W430, *transgrediens* Biozone, late Přídolí, ×10. **K**, *Bohemograptus praecornutus* Urbanek, ×8, AMF 102898, Black Bog Shale, Rainbow Hill, W830, Late Ludlow, *praecornutus* Biozone, ×8. **L,M**, *Neocucullograptus? yassensis* n.sp., holotype AMF 92343, Rosebank Shale, Derringullen Creek, W828, *parultimus* Biozone, Přídolí, ×20, L, AMF 92343a; M, counterpart AMF 92343b.

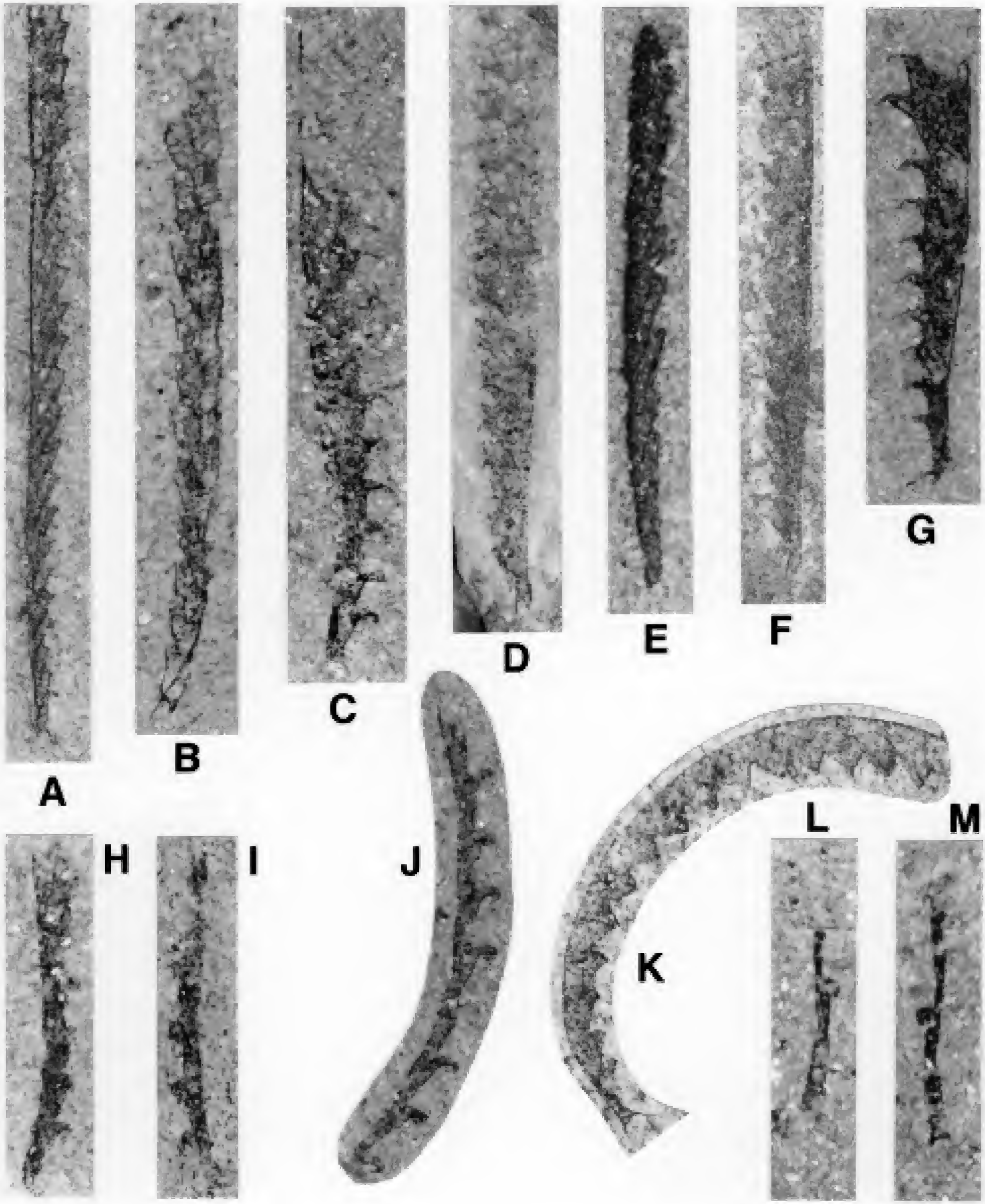


Figure 13. **A**, *Monograptus transgrediens* Perner. AMF 102927, Elmside Formation, Black Range Road, NW of Yass, W430, *transgrediens* Biozone, late Přídolí, ×5. **B**, *Pristiograptus shearsbyi* n.sp., paratype AMF 102925, Elmside Formation, Black Range Road, NW of Yass, W430, *transgrediens* Biozone, late Přídolí, ×10. **C**, *Monograptus bouceki* Přibyl, AMF 44608 (figured by Brown & Sherrard, 1952 as *Monograptus salweyi*), Cowridge Siltstone, Barambogie Creek, Přídolí, ×10. **D**, *Monograptus pridoliensis* Přibyl, AMF 92352, Rosebank Shale, W827, *parultimus* Biozone, Přídolí, ×10. … [Caption continued on p. 208, opposite]

COLLECTION LEVEL 4. The next highest graptolite level, based on localities W171, W827 and W828, is unquestionably referable to the *parultimus* Biozone at the base of the Přídolí. The assemblage in the Rosebank Shale is quite rich, although several taxa occur a little higher than expected. The *parultimus* assemblage appears some 20 m above the base of the Rosebank Shale; thus the interval between collection level 3 (assigned above to the *cornutus* Biozone) and the *parultimus* Biozone is occupied by the Rainbow Hill Marl Member (formerly known as the Middle Trilobite Bed) and an overlying sequence of approximately 20 m of siltstone, shale and fine to medium sandstone. In terms of graptolite biozones this barren 20 m might be roughly the equivalent of the *inexspectatus* and *kozlowski* biozones, but it has yielded no graptolites to us (see Appendix 1 for a fuller discussion of the stratigraphic position of this level).

The base of the Přídolí is, therefore, located some 20 m above the base of the Rosebank Shale, and is marked by the incoming of a striking *parultimus* fauna. The fauna has some unusual features. Firstly, *Crinitograptus* Rickards, 1995 is recorded for the first time in the Přídolí; the species *C. operculatus* Münch, 1938 has been previously recorded from the late Ludlow of northwest mainland Europe. There are also two new minuscule graptolites which we questionably place in *Neocucullograptus* Urbanek, 1970 as *N.? yassensis* n.sp. and *N.? mitchelli* n.sp. The genus has not previously been recorded from the Přídolí and the two new forms are diminutive graptolites even by the standards of the genus.

COLLECTION LEVEL 5. One other locality, shown on Fig. 2 as W835, is the locality in the Rosebank Shale in Reedy Creek (see Fig. 1) from which Brown & Sherrard (1952) described a poorly preserved specimen as *M. vomerinus* (Nicholson); the only specimen we collected from this unlikely locality is ?*M. parultimus*.

COLLECTION LEVEL 6. Localities W832 and W833 are low in the Cowridge Siltstone at "Tulla Park" (Fig. 2) just N of the Good Hope Road. Details of the sparse fauna are given in the appendix; the fauna belongs, like level four, to the *parultimus* Biozone.

COLLECTION LEVEL 7. Locality W834 is in the Cowridge Siltstone in Barambogie Creek. Jaeger (1967) referred the latter level to the *bouceki* Biozone on the presence of the eponymous species, *M. bouceki*, and two forms of *M. transgrediens*. We comment in the Systematic palaeontology section on the latter species provisionally recognising, only *M. transgrediens transgrediens*. We concur with the *bouceki* Biozone attribution which leaves about 30 m of siltstones and sandstones, as yet barren of graptolites, which might be roughly equivalent to the (unproven) *ultimus* and *lochkovensis* biozones of other sequences in the world.

COLLECTION LEVEL 8. Locality W430, in the basal Elmside Formation on Black Range Road (Jenkins, 1982), is almost certainly referable to the latest Přídolí *transgrediens* Biozone. This is the conclusion reached by Jenkins (1982) who interpreted the early form *M.* cf. *angustidens* Přibyl, 1940 (typically low Devonian) as an evolutionary transient from *M. bouceki* to *M. uniformis angustidens*. We reidentify this form as *M. hornyi* Jaeger *in* Kříž *et al.* (1986), a typical Přídolí species. The presence of *M. transgrediens* also suggests a Přídolí age. The *perneri* Biozone, between *bouceki* and *transgrediens* has not been proved in this work, but there is some 50 m of siltstone and sandstone in between the two proven horizons. Jenkins (1982, p. 172) concluded that the base of the Devonian lies at about the middle of the Elmside Formation, between the (lower) sandy unit and the (overlying) shaley unit with limestone lenses yielding the diagnostic Lochkovian conodont *Icriodus woschmidti* (Fig. 2) as identified by Link & Druce (1972).

Biostratigraphy and evolution of the Yass graptolites

Dendroid graptolites. The rare, fragmentary dendroid rhabdosomes are quite well preserved, allowing observation of autothecal details of *Dictyonema* sp. cf. *D. sherrardae* and *D. elegans* Bulman, 1928. The former may be best regarded as the end member of a long-ranging species, first appearing in the *nilssoni* Biozone (Rickards *et al.*, 1995).

Dictyonema elegans is a very long-ranging species appearing in the late Wenlock of the UK; its range was extended into the *nilssoni* Biozone by Rickards *et al.* (1995), and then into the late Ludlow by Rickards & Wright (1997). The autothecal spacing changes up sequence (25 in the Wenlock and early Ludlow; 30 in the *praecornutus* and *cornutus* biozones; and 20 in the very latest Ludlow specimens). When more and better preserved material is available it seems likely that "*D. elegans*" will be divisible into several taxa.

Linograptids. *Linograptus posthumus introversus* Rickards & Wright, 1997 was first described from latest Ludlow strata near Wellington (N.S.W.), so the slightly earlier record herein from the *cornutus* level extends the range slightly; it has only been recorded elsewhere from Romania at about the same level (Rickards & Iordan, 1975). *Linograptus p. introversus* is best considered a short-lived, late Ludlow offshoot of the long-ranging (low Ludlow to Early Devonian), cosmopolitan *L. p. posthumus* (Richter, 1875) as both exhibit thecal introversion; it may prove to have some stratigraphic value. The only other endemic Australian form, the very early Ludlow (*nilssoni* Biozone) *L. orangensis* Rickards *et al.*, 1995 from the Quarry Creek area (N.S.W.), was transferred by Rickards & Wright (1997) to their new genus *Prolinograptus*. *Linograptus posthumus tenuis* Jaeger, 1959 from the Silurian (early Ludlow) *scanicus* Biozone of Thuringia differs in being a tiny form.

Bohemograptids. We have elsewhere (Rickards & Wright 1999) given an account of bohemograptid evolution in a fully global context; in summary, we recognise two main lines of evolution:

1. The *Bohemograptus bohemicus bohemicus* to *B. b. tenuis* line (of which we see late members in the Yass sequence at collection levels two and three); and
2. The *Bohemograptus cornutus* line (of which we record here *B. praecornutus* and its derivative *B. paracornutus*). The appearance of a trumpet-shaped sicula, as in *B. paracornutus*, is a feature seen in only a few lineages (e.g., *Saetograptus fritschi linearis* (Bouček, 1936) and *Monograptus deubeli* Jaeger, 1959) below the Devonian (where, typically, it appears in the *hercynicus* and related lines), and never to the bizarre extent as in *B. paracornutus*.

Pristiograptids. Jaeger (1967, p. 282) noted that "morphologically advanced forms of the long-ranging group of *M. dubius* have been found". However, in the absence of figures, descriptions or specimens (see previous comments about Jaeger's Australian collections) it is difficult to know to what he was referring. From W830 at Rainbow Hill (i.e. *praecornutus* Biozone) we have obtained *Pristiograptus dubius* (Suess, 1851) itself, which is known to range into the Přídolí (see Koren′ & Sujarkova, 1997). We illustrate the form as Figs. 3G–I and note, in our description below, that the sicula has a pronounced dorsal tongue, much more so than in earlier Ludlow forms. It may be this form to which Jaeger referred. However, in the same beds, but more long-ranging overall at Yass (Fig. 2) is *P. shearsbyi* n.sp., a much more slender species than *P. dubius*, but also possessing a (short) dorsal sicular tongue. Jaeger (1967) did not refer to this form and may well have missed it on Barambogie Creek, where it is common and whence he recorded *M. bouceki* and *M. transgrediens*. It seems likely that *P. shearsbyi* is a gracile offshoot of the stem lineage of *P. dubius*; such slender species (as well as broad species) were derived repeatedly from the *P. dubius* lineage from the low Wenlock to the latest Ludlow (Rickards *et al.*, 1977, fig. 31), and most were short-lived species rarely lasting more than a couple of zones. By comparison (Fig. 2) *P. shearsbyi* was rather long-lived for such a form, ranging from the *praecornutus* zone (late Ludlow) to the *transgrediens* zone (late Přídolí).

Pristiograptus kolednikensis Přibyl, 1940 is here distinguished from the late Ludlow *P. fragmentalis* (Bouček, 1936) largely because it is less robust (maximum width 2 mm) and has a lower Σ value. *Pristiograptus fragmentalis* is much more commonly recorded, globally speaking, and our specimens do resemble *P. fragmentalis* as illustrated by Koren′ & Sujarkova (1997). The Yass material is, however, noticeably narrower and fits Přibyl's description of *P. kolednikensis* well. Both species must be related to *P. dubius*, but the proximal ends of both are straighter and the earlier thecae are inclined to the rhabdosomal axis at a higher angle. They are best considered late, robust offshoots of the stem lineage of *P. dubius*. The exact horizon of *P. kolednikensis* in Europe is in some doubt, but at Yass it occurs in the *parultimus* Biozone, which is above the range of *P. fragmentalis*. It is thus tempting to suggest that the Přídolí *P. kolednikensis* is a late derivative of *P. fragmentalis* rather than a direct offshoot of *P. dubius*; both differ from *dubius* in their high angle of inclination of th 1 (40–45°), whereas in *dubius* the angle is 20–30°.

Monograptids. *Monograptus pridoliensis* Přibyl, 1981. The evolutionary setting of this species was last discussed by Rickards & Garratt (1990). They supported Koren′'s (1983) proposition that a likely lineage was of *M. pridoliensis* → *M. prognatus* (both Přídolí) → *M. uniformis angustidens* (early Devonian). As Jenkins (1982) and Rickards & Garratt (1990) have shown, *M. uniformis*-like forms do occur in the late Přídolí (respectively *M.* cf. *angustidens* and *M. u.* cf. *parangustidens*). The stratigraphic occurrences of these species, and their morphological features suggest an evolutionary lineage as follows: *M. pridoliensis* (=*M. similis* Přibyl, 1940) in the early Přídolí; leading to *M. prognatus* and *M. bouceki* in the mid-Přídolí; and thence to early morphotypes of *M. uniformis* in the latest Přídolí. The changes involved are relatively subtle and include less biformity of the thecal hoods in the latest forms and an increase in the Σ values as the proximal end becomes more robust (Koren′, 1983).

Monograptus perneri elmsidensis n.subsp. is close to but narrower than the type subspecies and *M. p. kasachstanensis* Mikhajlova, 1975: in view of its occurrence in the latest Přídolí *transgrediens* Biozone, it seems best to regard it as a very late, rare form derived from *M. p. perneri* (*perneri* Biozone, late Přídolí) which it resembles in general rhabdosomal form. *Monograptus formosus jenkinsi* n.subsp., again from the latest Přídolí *transgrediens* Biozone, may well be a late derivative of *M. f. formosus* which occurs in the *parultimus* Biozone at Yass and ranges from late Ludlow to early Přídolí in Europe (Jaeger, in Kříž *et al.*, 1986).

ACKNOWLEDGMENTS. We are grateful for assistance from: Tim Munson and Bob Jones, for access to collections; property owners in the Yass district who allowed access to properties; Gordon Packham, Lawrence Sherwin and Des Strusz for valuable discussions; Hilary Alberti, David Martin and Richard Miller for production of figures; University of Wollongong palaeontology students who kindly donated important specimens; and valuable comments from reviewers. This paper is a contribution to IGCP Project 421: *North Gondwanaland mid-Palaeozoic bioevent/ biogeography patterns in relation to crustal dynamics*.

References

Barrande, J., 1850. *Graptolites de Bohême*. Prague.

Bassler, R., 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bulletin of the United States National Museum* 92: 1–718.

Bouček, B., 1931a. Deux contributions à la connaissance de la paléontologie et de la stratigraphie des zones à Graptolites du Gothlandien de la Bohême. *Věstník Státního Geologického Ústavu Československé Republiky* 7: 174–181.

Bouček, B., 1931b. Předbeza zpráva o nìkterych nových druzich graptolitù českego gotlandienu. *Věstník Státního Geologického Ústavu Československé Republiky* 7: 293–313.

Bouček, B., 1936. Graptolitová fauna českého spondního ludlowii. *Rozpravy České Akademie* 46: 1–26.

Bronn, H.G., 1835. *Lethaea geognostica*. Stuttgart, E. Schweitzerbartsche.

Bronn, H.G., 1849. *Index Palaeontologicus B. Enumerator palaeontologicus*. Stuttgart, E. Schweitzerbartsche.

Brown, I.A., 1941. The stratigraphy and structure of the Silurian and Devonian rocks of the Yass-Bowning district, N.S.W. *Journal and Proceedings of the Royal Society of New South Wales* 74: 312–341.

Brown, I.A., & K.M. Sherrard, 1952. Graptolite zones in the Silurian of the Yass-Bowning district of New South Wales. *Journal and Proceedings of the Royal Society of New South Wales* 85: 127–134.

Bulman, O.M.B., 1928. *A Monograph of the British Dendroid Graptolites*. Parts I–IV. *Palaeontographical Society Monographs* i–ixiv, 1–97, 1927–1967.

Cramsie, J., D.J. Pogson & C.J. Baker, 1978. *Geology of the Yass 1:100 000 sheet. 8628*. Sydney, New South Wales Geological Survey.

Frech, F., 1897. *Lethaea geognostica. Teil 1, Lethaea palaeozoica, 1 Bd., Graptolithiden* (Lief. 1–2 by F. Roemer; Lief. 3 by F. Frech), 544–684. Stuttgart, E. Schweitzerbartsche.

Geinitz, H.R., 1852. *Die Versteinerungen der Grauwacken-Formation (Die Graptolithen)*. Leipzig, Verlagwilhelm Engelmann.

Hall, J., 1843. Geology of New York, IV, Survey of the Fourth Geological District. Natural History of New York. New York.

Hall, J., 1851. New genera of fossil corals. *American Journal of Science* 11: 398–401.

Hall, J., 1858. Description of Canadian Graptolites. *Geological Survey of Canada, Report for 1857*, 111–145.

Hall, J., 1862. New species of fossils from the investigations of the Survey. *Wisconsin Geological Survey, Report for 1861*, 1–18.

Hall, T.S., 1903. On the occurrence of *Monograptus* in New South Wales. *Proceedings of the Linnean Society of New South Wales* 27: 654–655.

Hopkinson, J. in Lapworth, C., 1880. On new British graptolites. *Annals and Magazine of Natural History*, series 5, 5: 149–177.

Howe, M., 1983. Measurement of thecal spacing in graptolites. *Geological Magazine* 120: 635–638.

Jaeger, H., 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. *Abhandlungen der Deutschen Akademie der Wissenschaft zu Berlin* 2: 1–197.

Jaeger, H., 1967. Preliminary stratigraphical results from graptolite studies in the Upper Silurian and Lower Devonian of southeastern Australia. *Journal of the Geological Society of Australia* 14: 281–286.

Jaeger, H., 1975. Die Graptolithenführung in Silur/Devon des Cellon-Profils (Karnische Alpen). *Carinthia* II, 165/185: 111–126.

Jaeger, H., 1991. Neue Standard-Graptolithenfolge nach der "Grossen Krise" an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 182: 303–354.

Jaekel, O., 1889. Über das Älter des sogen. Graptolithengesteins. *Zeitschrift der Deutschen Geologischen Gesellschaft* 41: 653–716.

Jell, J.S., & J.A. Talent, 1989. Australia: the most instructive sections. In *A global standard for the Silurian System*, eds. C.H. Holland & M.G. Bassett, pp. 183–200. *National Museum of Wales, Geological Series* 10. Cardiff.

Jenkins, C.J., 1982. Late Pridolian graptolites from the Elmside Formation near Yass, New South Wales. *Proceedings of the Linnean Society of New South Wales* 106: 167–172.

Koren′, T.N., 1983. New late Silurian monograptids from Kazakhstan. *Palaeontology* 26: 407–434.

Koren′, T.N., 1986. Graptolites. In *Balkhashski segment. Tokrauski horizont verkhnego silura*, eds. I.F. Nikitin & S.M. Bandaletov, pp. 86–138. Nauka Kazakhskoi SSR, Alma Ata.

Koren′, T.N., 1993. The key levels in the evolution of the Ludlow graptolites. *Stratigrafia Geologicheskaya Korreljatsia* 1(5): 44–52.

Koren′, T.N., & A.A. Sujarkova, 1997. Late Ludlow and Přídolí monograptids from the Turkestan-Alai Mountains, South Tien-Shan. *Palaeontographica* 247A: 59–90.

Kraft, J., 1984. Post-Lochkovian dendroid graptolites from the Devonian of Central Bohemia. *Časopis pro mineralogii a geologii* 29: 115–127.

Kříž, J., H. Jaeger, F. Paris & H.P. Schönlaub, 1986. Přídolí—the Fourth Subdivision of the Silurian. *Jahrbuch der Geologischen Bundesanstalt* 129: 291–360.

Kühne, W.G., 1955. Unterludlow-Graptolithen aus Berliner Geschieben. *Abhandlungen der Neues Jahrbuch für Geologie und Paläontologie* 100: 350–410.

Lapworth, C., 1873. On an improved classification of the Rhabdophora. *Geological Magazine*, series 1, 10: 500–504, 555–560.

Lapworth, C., 1875. In *Descriptions of the graptolites of the Arenig and Llandeilo rocks of St Davids*, eds. J. Hopkinson & C. Lapworth. *Quarterly Journal of the Geological Society of London* 31: 631–672.

Lenz, A.C., 1990. Ludlow and Přídolí (Upper Silurian) graptolite biostratigraphy of the central Arctic Islands: a preliminary report. *Canadian Journal of Earth Sciences* 27: 1074–1083.

Link, A.G., 1970. Age and correlations of the Siluro-Devonian strata in the Yass Basin. *Journal of the Geological Society of Australia* 16: 711–722.

Link, A.G., & E.C. Druce, 1972. Ludlovian and Gedinnian conodont stratigraphy of the Yass Basin, New South Wales. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics (Australia)* 134: 1–136.

Mikhajlova, N.F., 1975. Graptolites. In *Characteristic faunas of the Silurian/Devonian boundary beds in Central Kazakhstan*, ed. V.V. Menner. *Materialy po geologii Zentralnogo Kazakhstana* 12: 151–158.

Miller, S.A., 1889. *North American Geology and Paleontology*. Cincinnati, Ohio, Western Methodist Book Concern.

Mitchell, J., 1886. Notes and exhibits. *Proceedings of the Linnean Society of New South Wales* (Second Series) 1: 577.

Mitchell, J., 1888. Notes and exhibits. *Proceedings of the Linnean Society of New South Wales* (Second Series) 3: 150.

Münch, A., 1938. Einige grundlegerde Fragen über Bau und Strukture von *Monograptus* Gein. und *Barrandeograptus* Bouc. *Zeitschrift für Geschiebeforschung und Flachland-geologie* 14: 31–63.

Nicholson, H.A., 1872. *Monograph of British Graptolites* i–x, 1–133. Edinburgh & London, Blackwood & Sons.

Packham, G.H., 1962. Some Diplograptids from the British Lower Silurian. *Palaeontology* 5: 498–526.

Packham, G.H., 1968. *Monograptus* cf. *ultimus* Perner and *Monograptus formosus* Bouček from the Hume Series of the Yass District, New South Wales. *Proceedings of the Linnean Society of New South Wales* 92: 217–221.

Perner, J., 1899. Études sur les Graptolithes de Bohême. III. Monographie des Graptolithes de l'Étage E. Section b. Leipzig, Raimund Gerhard.

Porebska, E., 1984. Latest Silurian and early Devonian Graptolites from Zdanów Section, Bardo Mts. (Sudetes). *Annale Societatis Geologorum Poloniae* 52: 89–209.

Přibyl, A., 1940. Revise českých graptolitù rodu *Monoclimacis*, Frech. *Rozpravy České Akademie* 50: 1–19.

Přibyl, A., 1943. Revision aller Vertreter der Gattung *Pristiograptus* aus der Gruppe *P. dubius* und *P. vulgaris* aus dem böhmischen und ausländischen Silur. *Bulletin International de l'Académie Tchéque des Sciences* 44: 33–81.

Přibyl, A., 1967. O rodu *Bohemograptus* gen. nov. (Graptoloidea) z Českého a ciziho ludlowu. *Časopis Národního Musea* 136: 133–136.

Přibyl, A., 1981. New graptolites of the family Monograptidae from the Upper Silurian. *Věstník Ústedniho Ústavu geologického* 5G: 371–375.

Prout, A.H., 1851. Description of a new graptolite found in the Lower Silurian rocks near the falls of St. Croix River. *American Journal of Science* 11: 187–191.

Richter, R., 1875. Aus dem thüringischen Schiefergebirge V. *Zeitschrift der Deutschen Geologischen Gesellschaft* 27: 261–273.

Rickards, R.B., 1995. *Crinitograptus*, a new genus of Ludlow (Silurian) graptoloid. *Journal of Paleontology* 69: 1107–1111.

Rickards, R.B., & M.R. Banks, 1992. Two *Monograptus* species from the Přídolí of western Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 126: 9–11.

Rickards, R.B., & M.J. Garratt, 1990. Přídolí graptolites from the Humevale Formation at Ghin Ghin and Cheviot, Victoria, Australia. *Proceedings of the Yorkshire Geological Society* 48: 41–46.

Rickards, R.B., Hutt, J.E. & Berry, W.B.N., 1977. Evolution of the Silurian and Devonian graptoloids. *Bulletin of the British Museum (Natural History), Geology* 28: 3–120.

Rickards, R.B., & M. Iordan, 1975. Rumanian graptolites from boreholes in the Moesias Platform. *Geological Magazine* 112: 241–255.

Rickards, R.B., G.H. Packham, A.J. Wright & P.L. Williamson, 1995. Wenlock and Ludlow graptolite faunas and biostratigraphy of the Quarry Creek district, N.S.W. *Association of Australasian Palaeontologists Memoir* 17: 1–68.

Rickards, R.B., & A.J. Wright, 1997. Graptolites from the Barnby Hills Shale (Silurian, Ludlow), New South Wales, Australia. *Proceedings of the Yorkshire Geological Society* 51: 209–227.

Rickards, R.B., & A.J. Wright, 1999. Evolution of the Ludlow (Silurian) graptolite genus Bohemograptus Přibyl 1936. *Proceedings of the Yorkshire Geological Society* 53: 313–320.

Roemer, 1897. (See under Frech, 1897).

Shearsby, A.J., 1912. The geology of the Yass district. *Reports of the Australian and New Zealand Association for the Advancement of Science* 13: 106–119.

Sherrard, K.M., 1960. Some Silurian lamellibranchs from New South Wales. *Proceedings of the Linnean Society of New South Wales* 84: 356–372.

Sherrard, K.M., & R.A. Keble, 1937. The occurrence of graptolites near Yass, New South Wales. *Proceedings of the Linnean Society of New South Wales* 62: 303–314.

Sherwin, L., 1979. Late Ordovician to Early Devonian graptolite sequences in Australia. *Acta Palaeontologica Polonica* 24: 155–163.

Štorch, P., 1995. Upper Silurian (upper Ludlow) graptolites of the *N. inexspectatus* and *N. kozlowskii* biozones from Kosov quarry near Beroun (Barrandian area, Bohemia). *Věstník Českého Geologického Ústavu* 70: 65–89.

Strzelecki, P.E. de, 1845. *Physical Description of New South Wales and Van Diemens Land, Accompanied by a Geological Map, Sections and Diagrams*. London, Lonman, Brown, Green and Longmans.

Suess, E., 1851. Über böhmische Graptolithen. *Naturwissenschaftenliche Abhandlungen* (von W. Haidinger) 4: 87–134.

Teller, L., 1964. Graptolite fauna and stratigraphy of the Ludlovian deposits from the Chelm bore-hole (E. Poland). *Studia Geologica Polonica* 13: 1–88.

Teller, L., 1966. Two species of Monograptidae from the upper Ludlovian of Poland. *Bulletin de l'Académie Polonaise des Sciences* 14: 557–558.

Teller, L., 1997. Revision of certain Přídolí Monograptids from the Chelm Key section (EEP). *Palaeontologica Polonica* 56: 71–85.

Tsegelnjuk, P.D., 1976. Late Silurian and early Devonian monograptids from the south-western Ukrainian East-European Platform. In *Palaeontology and Stratigraphy of the upper Precambrian and lower Palaeozoic of the south-west part of the East European Platform*, ed. P.L. Shalga, pp. 91–133. Kiev, Naukova Dumka.

Tsegelnjuk, P.D., 1988. Graptoliti gruppi *Monograptus ludensis* (Murchison, 1839) iz Silura Volini. Podolii (Graptolites of the *Monograptus ludensis* (Murchison, 1839) group from the Silurian of Volynia and Podolia). Graptolites in the Earth History: Abstracts for the 5th Symposium on investigation of graptolites in the USSR, 81–83. Vilnius.

Urbanek, A., 1958. Monograptidae from erratic boulders of Poland. *Palaeontologica Polonica* 9: 1–105.

Urbanek, A., 1970. Neocucullograptinae n. subfam. (Graptolithina) —their evolutionary and stratigraphic bearing. *Acta Palaeontologica Polonica* 15: 163–393.

Urbanek, A., 1997. Late Ludfordian and early Přídolí monograptids from the Polish lowland. *Palaeontologica Polonica* 56: 87–231.

Urbanek, A., & L. Teller, 1997. Graptolites and stratigraphy of the Wenlock and Ludlow Series in the East European Platform. *Palaeontologica Polonica* 56: 23–57.

Wood, E.M.R., 1900. The Lower Ludlow formation and its graptolite fauna. *Quarterly Journal of the Geological Society of London* 56: 415–492.

Manuscript received 1 September 1998, revised 2 August 1999 and accepted 3 August 1999.

Associate Editor: G.D. Edgecombe.

Appendix

Locality data for Yass localities cited

All collection sites (Fig. 1) are located on the Yass 1: 50 000 topographic sheet (8628-S), and all grid references (GR) refer to that sheet. With the exception of the first three localities below which were made earlier by AJW, all collections were made by the authors in December 1997.

W69 Black Bog Shale, Yarwood Siltstone Member (= "Lower Trilobite Bed" of Brown, 1941); Derringullen Creek, GR 713477. Ludlow. Apart from dendroids reported by Jaeger (1967) from low in the Black Bog Shale, and graptolites possibly from this horizon (Shearsby, 1912), this is the lowest known Ludlow graptolite from Yass. *Dictyonema* sp. cf. *D. sherrardae*; collected by AJW in 1972.

W171 Collected by AJW in 1974. GR 715472. This is probably the locality of Packham (1968) and Jaeger (1967) at the crossing of the highway and Derringullen Creek. The small quarry, probably that shown by Link & Druce (1972), was largely destroyed during the construction of the dual carriageway in the early 1970s. It appears to be very close stratigraphically to W827 and W828 (see below). The fauna is early Přídolí, belonging to the *parultimus* Biozone.

The locality lies perhaps as much as 30 m above the base of the Rosebank Shale. Because the Rainbow Hill Marl does not outcrop in this vicinity, the stratigraphic interval separating the Marl from the overlying fossiliferous level is uncertain. It was said by Packham (1968) to be "within a hundred feet" and a label accompanying a specimen in the Australian Museum and written by I.A. Browne states that the interval is as little as 20 ft (ca. 6 m); Jaeger (1967) stated that these beds yielding our *parultimus* fauna "have a maximum thickness of 30 m and immediately overlie the *Dalmanites* Bed" (i.e., the Rainbow Hill Marl Member). The collective fauna from this locality, W827 and W828, as well as taxa recorded by Packham and Jaeger, is: *Dictyonema* sp. cf. *D. sherrardae*; *Dictyonema* sp.; "*Medusaegraptus*" sp.; *Monograptus parultimus* Jaeger, 1975; *M. pridoliensis* Přibyl, 1981; *Monograptus formosus formosus* Bouček, 1931b; *Crinitograptus operculatus* (Münch, 1938); *Neocucullograptus? mitchelli* n.sp.; *Neocucullograptus? yassensis* n.sp.; *Linograptus posthumus posthumus* Richter, 1875; *Pristiograptus kolednikensis* Přibyl, 1940; and *Pristiograptus shearsbyi* n.sp. No associated fauna has been recorded from these localities, although possible plant fragments were noted.

W430 Black Range Road cutting in the lower part of the Elmside Formation (Jenkins, 1982); GR 696447. The sequence consists of alternating shale and fine micaceous sandstone beds; the latter have been the source of all our graptolites and commonly show HCS and shallow water sole markings. Associated fauna (see also Link & Druce, 1972) includes most commonly the brachiopod *Plectodonta bipartita* Chapman (normally cited as a senior synonym of

Plectodonta davidi Brown) occurring as abundant disarticulated, disoriented valves, and *Lissatrypa*; and rare trilobites such as *Kettneraspis rattei* (Etheridge & Mitchell). Large (up to ca. 10 mm) amorphous carbonaceous bodies also occur with the graptolites. The low diversity but well-preserved and abundant graptolite fauna is dominated by *Linograptus posthumus posthumus* and the monograptids: *Monograptus transgrediens* Perner, 1899; *Monograptus hornyi* Jaeger (*in* Kříž *et al*., 1986); *Monograptus perneri elmsidensis* n.subsp., a single specimen of *Monograptus formosus jenkinsi* n.subsp., and the dendroid *Dictyonema elegans* Bulman, 1928. This fauna is late Přídolí. First AJW collections made in 1982.

W827 Low bare shale outcrops on W bank of Derringullen Creek, upstream of motorway bridge. GR as for W171. This locality has yielded the *M. parultimus* fauna, which is listed in its entirety under W171. We have not collected *M. formosus* at this locality, nor at W828.

W828 This locality is about 15 m further W from W827 but has similarly been grouped with W171. GR as for W171 and W827.

W830 Rainbow Hill, about 15 m below the top of the Black Bog Shale; GR 712409; *praecornutus* Biozone, late Ludlow. Fauna includes: *Monograptus bohemicus tenuis* Bouček, 1936; *Monograptus praecornutus* Urbanek, 1970; *Pristiograptus shearsbyi* n.sp.; *Pristiograptus dubius* Suess, 1851; *Linograptus p. posthumus*; *Dendrograptus* sp.; and *Dictyonema elegans* Bulman, 1928.

W831 Rainbow Hill, uppermost 2–3 m of the Black Bog Shale; GR 712409. The fossiliferous strata are layered organic-rich shales with abundant pyrite on bedding planes, although the graptolites are not pyritised. Bedding planes are often covered with overlapping, complete, mature rhabdosomes. The associated very sparse fauna includes: the rare clams (Sherrard, 1960) *Cardiola, Pteronitella rugosa* Sherrard, 1960, *Actinopterella minuta* Sherrard, 1960; and rare small brachiopods, ceratiocarids, ostracodes, nautiloids and trilobite elements. The gradational contact with the shallow water marls of the Rainbow Hill Marl Member of the Rosebank Shale indicates a marked regression. Slight tectonic deformation has produced the normal different appearances of the fossils in the two extreme conditions. The graptolite fauna includes: *Dictyonema elegans*; *Dictyonema* sp. cf. *D. sherrardae*; *Linograptus posthumus posthumus*; *Linograptus posthumus introversus* Rickards & Wright, 1997; *Monograptus paracornutus* n.sp.; and *Monograptus bohemicus tenuis*. Contrary to the statement by Brown & Sherrard (1952), this *bohemicus* fauna was first found by Dr Gordon Packham in 1947 at Rainbow Hill and subsequently material was made available to Dr Ida Brown and Mr A.J. Shearsby (Gordon Packham, pers. comm., 1998). Note that there is some further confusion in locality data given by Brown & Sherrard (1952, p. 130).

W832, W833 Cowridge Siltstone, "Tulla Park", mostly from fine sandstone rubble low in formation, on low ridge west of farm track; GR 724385. The former locality is in the northern part of portion 15, the latter in the southern. This is presumably the "*salweyi*" horizon of Brown & Sherrard (1952, fig. 1). Fauna consists of: *Monograptus parultimus* Jaeger, 1975 and *Pristiograptus shearsbyi* n.sp. As indicated by Jaeger (1967) no monograptids with hooked thecae were found here.

W834 Cowridge Siltstone, Barambogie Creek, GR 693515; all material from float, but apparently derived from no lower than halfway up lower unit recognised by Link & Druce (1972). This locality is close to the "Silverdale" locality of Sherrard & Keble (1937) which was from a ridgetop (portion 34, parish of Derringullen) just N of the creek near the Yass-Boorowa road (Fig. 1). The photograph published by Brown & Sherrard (1952), purporting to be of this Silverdale locality, is a view of Rainbow Hill from the North. Fauna includes: *Dictyonema* sp., *Monograptus transgrediens, M.* sp., *M. bouceki* and *Pristiograptus shearsbyi*.

W835 Rosebank Shale, Reedy Creek. Collecting at this roadside locality was undertaken because Brown & Sherrard (1952) described material from (presumably) here as *Monograptus vomerinus* (Nicholson); our only poor material is a very doubtful *Monograptus parultimus*. GR 698372.

Records of the Australian Museum (1999) Volume 51. ISSN 0067-1975

CONTENTS

Volume 51 • Numbers 1–3 • 1999

Ayress, M., T. Barrows, V. Passlow & R. Whatley. Neogene to Recent species of *Krithe* (Crustacea: Ostracoda) from the Tasman Sea and off southern Australia with description of five new species 1
p. 1 http://www.amonline.net.au/pdf/publications/486.pdf
pp. 1–22 http://www.amonline.net.au/pdf/publications/486_complete.pdf

Barrows, T., see under Ayress.

Barwick, R.E., see under Campbell.

Bauer, A.M., see under Sadlier.

Brock, G.A. An unusual micromorphic brachiopod from the Middle Cambrian of north-eastern New South Wales, Australia 179
p. 179 http://www.amonline.net.au/pdf/publications/1305.pdf
pp. 179–186 http://www.amonline.net.au/pdf/publications/1305_complete.pdf

Campbell, K.S.W., & R.E. Barwick. A new species of the Devonian lungfish *Dipnorhynchus* from Wee Jasper, New South Wales 123
p. 123 http://www.amonline.net.au/pdf/publications/1301.pdf
pp. 123–140 http://www.amonline.net.au/pdf/publications/1301_complete.pdf

Castle, P.H.J., & J.E. McCosker. A new genus and two new species of myrophine worm-eels, with comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae) 113
p. 113 http://www.amonline.net.au/pdf/publications/1300.pdf
pp. 113–122 http://www.amonline.net.au/pdf/publications/1300_complete.pdf

Colgan, D.J., see under Sadlier.

Edwards, A.J., see under Gill.

Gill, A.G., & A.J. Edwards. Monophyly, interrelationships and description of three new genera in the dottyback fish subfamily Pseudoplesiopinae (Teleostei: Perciformes: Pseudo chromidae) 141
p. 141 http://www.amonline.net.au/pdf/publications/1302.pdf
pp. 141–160 http://www.amonline.net.au/pdf/publications/1302_complete.pdf

Halse, S.A., see under Knott.

Knott, B., & S.A. Halse. *Pilbarophreatoicus platyarthricus* n.gen., n.sp. (Isopoda: Phreatoicidea: Amphisopodidae) from the Pilbara Region of Western Australia 33
p. 33 http://www.amonline.net.au/pdf/publications/1291.pdf
pp. 33–56 http://www.amonline.net.au/pdf/publications/1291_complete.pdf

Larsen, K. Pacific Tanaidacea (Crustacea): revision of the genus *Agathotanais* with description of three new species 99
p. 99 http://www.amonline.net.au/pdf/publications/1299.pdf
pp. 99–112 http://www.amonline.net.au/pdf/publications/1299_complete.pdf

McCosker, J.E., see under Castle.

Müller, C.J. A new species of *Cethosia* and a new subspecies of *Delias* (Lepidoptera: Nymphalidae and Pieridae) from New Ireland, Papua New Guinea 169
p. 169 http://www.amonline.net.au/pdf/publications/1304.pdf
pp. 169–177 http://www.amonline.net.au/pdf/publications/1304_complete.pdf

Müller, C.J., & W.J. Tennent. A new species of *Graphium* Scopoli (Lepidoptera: Papilionidae) from the Bismarck Archipelago, Papua New Guinea 161
p. 161 http://www.amonline.net.au/pdf/publications/1303.pdf
pp. 161–168 http://www.amonline.net.au/pdf/publications/1303_complete.pdf

Passlow, V., see under Ayress.

Rickards, R.B., & A.J. Wright. Systematics, biostratigraphy and evolution of the late Ludlow and Prídolí (Late Silurian) graptolites of the Yass District, New South Wales, Australia 187
p. 187 http://www.amonline.net.au/pdf/publications/1306.pdf
pp. 187–214 http://www.amonline.net.au/pdf/publications/1306_complete.pdf

Sadlier, R.A., A.M. Bauer & D.J. Colgan. The scincid lizard genus *Caledoniscincus* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: a review of *Caledoniscincus austrocaledonicus* (Bavay) and description of six new species from Province Nord 57
p. 57 http://www.amonline.net.au/pdf/publications/1295.pdf
pp. 57–82 http://www.amonline.net.au/pdf/publications/1295_complete.pdf

Sadlier, R.A., & A.M. Bauer. The scincid lizard genus *Sigaloseps* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: description of a new species and review of the biology, distribution and morphology of *Sigaloseps deplanchei* (Bavay) 83
p. 83 http://www.amonline.net.au/pdf/publications/1296.pdf
pp. 83–91 http://www.amonline.net.au/pdf/publications/1296_complete.pdf

Sadlier, R.A., & A.M. Bauer. The scincid lizard *Lioscincus tillieri* (Reptilia: Scincidae) from New Caledonia in the Southwest Pacific: new information on the species' biology, distribution and morphology 93
p. 93 http://www.amonline.net.au/pdf/publications/1297.pdf
pp. 93–98 http://www.amonline.net.au/pdf/publications/1297_complete.pdf

Scheltema, A.H. Two solenogaster molluscs, *Ocheyoherpia trachia* n.sp. from Macquarie Island and *Tegulaherpia tasmanica* Salvini-Plawen from Bass Strait (Aplacophora: Neomenio morpha) 23
p. 23 http://www.amonline.net.au/pdf/publications/1266.pdf
pp. 23–31 http://www.amonline.net.au/pdf/publications/1266_complete.pdf

Shea, G.M. Waite's blind snakes (Squamata: Scolecophidia: Typhlopidae): identification of sources and correction of errors 43
p. 43 http://www.amonline.net.au/pdf/publications/1294.pdf
pp. 43–56 http://www.amonline.net.au/pdf/publications/1294_complete.pdf

Tennent, W.J., see under Müller.

Whatley, R., see under Ayress.

Wright, A.J., see under Rickards.

AUSTRALIAN
MUSEUM

Publications may be purchased at the Australian Museum Shop or online at:
www.amonline.net.au/shop/

INSTRUCTIONS TO AUTHORS

Manuscripts must be submitted to the Editor. Authors will then liaise with a nominated Associate Editor until a work is accepted, rejected or withdrawn. All manuscripts are refereed externally.

Only those manuscripts that meet the following requirements will be considered for publication.

Submit three hard copies and one electronic file. Attach a **cover sheet** showing: the title; the name, address and contact details of each author; the author responsible for checking proofs; a suggested running head of less than 40 character-spaces; the number of figures, tables and appendices; and total word count. Manuscripts must be complete when submitted.

Electronic copy is stripped and reconstructed during production, so authors should avoid excessive layout or textual embellishments; a single font should be used throughout (Times or Times New Roman are preferred). **Tables** and **figures** should be numbered and referred to in numerical order in the text.

All copy is manipulated within a Windows (not Mac) environment using Microsoft and Adobe software. Electronic submissions should be entirely readable using the latest version of Microsoft Word. Avoid using uncommon fonts. The submitted manuscript should be printed from the most recent version of electronic copy.

A manuscript should be prepared using recent issues as a guide. There should be a **title** (series titles should not be used), **author**(s) with their institutional and e-mail addresses, an **abstract** (should be intelligible by itself, informative not indicative), **introduction** (should open with a few lines for general, non-specialist readers), **materials and methods**, **results** (usually subdivided with primary, secondary and sometimes tertiary-level headings), **discussion**, **acknowledgments** and **references**. If appropriate, an appendix may be added after references. An index may be called for if a paper is very large (>55,000 words) and contains many indexible elements.

In the **titles** of zoological works the higher classification of the group dealt with should be indicated. Except for common **abbreviations**, definitions should be given in the materials and methods section. Sentences should not begin with abbreviations or numerals. Metric units must be used except when citing original specimen data. It is desirable to include **geo-spatial coordinates**; when reference is made to them, authors must ensure that their format precludes ambiguity, in particular, avoid formats that confuse arcminutes and arcseconds. If known, authors should indicate how geo-spatial coordinates are derived, for example, from GPS, map, gazetteer, sextant, or label.

Label and specimen data should, as a minimum requirement, indicate where specimens are deposited. Original specimen data—especially that of type material—is preferred over interpreted data. If open to interpretation, cite original data between quotation marks or use "[sic]".

Rules of the most recent edition of the International Code of Zoological Nomenclature must be followed; authors must put a very strong case if Recommendations are not followed. Authorities, including date, should be given when a specific name is first mentioned except where **nomenclature** follows an accepted standard (in which case that standard should then be cited). When new taxa are introduced in works having **multiple authors**, the identity of the author(s) responsible for the new name(s) and for satisfying the criteria of availability, should be made clear in accordance with recommendations in Chapter XI of the Code (1985). In the view of the Editorial Committee, a scientific name with more than two authors is unwieldy and should be avoided. **Keys** are desirable; they must be dichotomous and not serially indented. **Synonymies** should be of the short form: taxon author, year, pages and figures. A period and dash must separate taxon and author except in the case of reference to the original description. Manuscripts will not be accepted for publication until registration numbers or unique identifiers are provided for holotype and all paratype specimens.

Authors should retain **original artwork** until it is called for. Previously published illustrations will generally not be accepted. Artwork may be submitted either as hard copy or as **digital images**. The author, figure number and orientation must be clearly marked on each piece of artwork. Extra costs resulting from **colour** production are charged to the author. All artwork must (*a*) be rectangular or square and scalable to a width of 83 mm (one text column) or 172 mm (both text columns) and any depth up to 229 mm (the number of lines in a caption limits depth); (*b*) have **lettering** similar to 14 point upper case normal Helvetica in final print; and (*c*) have **scale bars**, the lengths of which should be given in the caption.

Hard copy submissions must meet the following requirements: (*a*) if larger than A4 they must be on media that can be shaped to fit a drum scanner and they must have a >20 mm working space around the outside; (*b*) the dimension of artwork should not be less than the desired final size; (*c*) **halftones** and **line-drawings** must be mounted separately; (*d*) lettering and edges—especially of halftone artwork—must be sharp and straight; (*e*) photographic **negatives** can be used during production, but *positive* images are, of course, required by referees.

Halftone, colour or black and white line images may be submitted electronically; all such images must be presented in a file format, such as TIFF, suitable for *Adobe Photoshop* version 5.0 or later. Halftone and colour images must be at a minimum **resolution** of 300 dpi (not higher than 400 dpi) at final size and all labelling must be sharp. Black and white line images must be at a minimum resolution of 1200 dpi at final size.

When reference is made to **figures** in the present work use Fig. or Figs., when in another work use fig. or figs.; the same rule applies to tables. Figures should be numbered and referred to in numerical order in the text.

Authors should refer to recent issues of the *Records of the Australian Museum* to determine the correct format for listing **references** and to *The Chicago Manual of Style* to resolve other matters of style.

Certain **anthropological manuscripts** (both text and images) may deal with culturally sensitive material. Responsibility rests with authors to ensure that approvals from the appropriate person or persons have been obtained prior to submission of the manuscript.

Stratigraphic practice should follow the *International Stratigraphic Guide* (second edition) and *Field Geologist's Guide to Lithostratigraphic Nomenclature in Australia*.

The Editor and Publisher reserve the right to modify manuscripts to improve communication between author and reader. Authors may make essential corrections only to final **proofs**. No corrections can be accepted less than six weeks prior to publication without cost to the author(s). All proofs should be returned as soon as possible. There are no page **charges**. Authors of a paper in the *Records* receive a total of 50 free **offprints**. Authors of a *Supplement* or *Technical Report* receive a total of 25 free offprints. Additional offprints may be ordered at cost.

All authors must agree to publication and certify that the research described has adhered to the Australian Museum's *Guidelines for Research Practice* (http://www.austmus.gov.au/resethics.htm)—or those of their home institution providing they cover the same issues, especially with respect to authorship and acknowledgment. Agreement can be registered by signing and returning the Editor's letter that confirms our receipt of a submitted manuscript. While under consideration, a manuscript may not be submitted elsewhere.

More information is available at our web-site:

http://www.austmus.gov.au/info/pub.htm

ALSO AVAILABLE FROM THE PUBLISHER

Records of the Australian Museum 32 (1979). $10.00

Cogger, H.G., 1979. Type specimens of reptiles and amphibians in the Australian Museum. Pp. 163–210. Stock no. 979R32B.

Records of the Australian Museum 32 (1979). $10.00

Greer, Allen E., 1979. *Eremiascincus*, a new generic name for some Australian sand swimming skinks (Lacertilia: Scincidae). Pp. 321–338. Stock no. 979R32C.

—— 1979. A phylogenetic subdivision of Australian skinks. Pp. 339–371. Stock no. 979R32C.

—— 1979. A new *Sphenomorphus* (Lacertilia: Scincidae) from the rainforests of northeastern Queensland. Pp. 373–383. Stock no. 979R32C.

—— 1979. A new species of *Lerista* (Lacertilia: Scincidae) from northern Queensland, with remarks on the origin of the genus. Pp. 383–388. Stock no. 979R32C.

Records of the Australian Museum 33 (1980). $10.00

Greer, Allen E., 1980. A new species of *Morethia* (Lacertilia: Scincidae) from northern Australia, with comments on the biology and relationships of the genus. Pp. 89–122. Stock no. 980R33A.

Records of the Australian Museum 35 (1983). $33.00

Greer, Allen E., 1983. The Australian scincid lizard genus *Calyptotis* De Vis: Resurrection of the name, description of four new species, and discussion of relationships. Pp. 29–59. Stock no. 983R35A.

Records of the Australian Museum 37 (1985). $33.00

Greer, Allen E., & Harold G. Cogger, 1985. Systematics of the reduce-limbed and limbless skinks currently assigned to the genus *Anomalopus* (Lacertilia: Scincidae). Pp. 11–54. Stock no. 985R37A.

Records of the Australian Museum 39 (1987). $33.00

Sadlier, Ross A., 1987. A review of the scincid lizards of New Caledonia. Pp. 1–66. Stock no. 987R39A.

Records of the Australian Museum, Supplement 19 (1993). $30.00

Kluge, Arnold G., 1993. *Aspidites* and the phylogeny of pythonine snakes. Pp. 1–77. Stock no. 993S19.

Records of the Australian Museum 47(1) (1995). $33.00

Shea, Glenn M., 1995. A taxonomic revision of the *Cyclodomorphus casuarinae* complex (Squamata: Scincidae). Pp. 83–115. Stock no. 995R47A.

Records of the Australian Museum 47(3) (1995). $33.00

Shea, Glenn M., & Brian Miller, 1995. A taxonomic revision of the *Cyclodomorphus branchialis* species group (Squamata: Scincidae). Pp. 265–325. Stock no. 995R47C.

Technical Reports of the Australian Museum 15 (1999). $25.00

Shea, Glenn M., & Ross A. Sadlier, 1999. A catalogue of the non-fossil amphibian and reptile type specimens in the collection of the Australian Museum: Types currently, previously and purportedly present. Stock no. 999T15.

AM

AUSTRALIAN MUSEUM

Prices are in Australian Dollars (AUD). Payments by Visa, MasterCard and American Express are accepted. Please add 10% for postage and handling within Australia or 20% for other countries. Send orders or enquiries to Ms Karen Hilliger, Scientific Publications, Australian Museum, 6 College Street, Sydney NSW 2000, Australia; fax +612 9320 6073, editor@amsg.austmus.gov.au or visit our website http://www.austmus.gov.au/info/pub.htm

RECORDS OF THE AUSTRALIAN MUSEUM 1999 Vol. 51 Nos. 2 & 3